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MECHANISMS OF WOMEN'S OWN-GENDER BIAS AND SEX DIFFERENCES IN MEMORY FOR FACES

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To Håkan, my family, and other animals

ABSTRACT

There are sex differences in some cognitive functions. For example, earlier studies have shown that women outperform men on face recognition tasks, and women, in contrast to men, show an own-gender bias (i.e., women typically recognize more female than male faces). In the present thesis, the role of puberty, sex hormones, and attention, as well as neural correlates of the sex difference and women's own-gender bias in face recognition were investigated.

In **Study I**, the aim was to determine whether sex differences in cognitive abilities are magnified during early adolescence (ages 12-14), as a function of differences in age, hormone levels, and/or pubertal development. The results showed that boys' advantage in mental rotations and girls' advantage in verbal fluency, verbal episodic memory, and face recognition memory were not magnified during this age period, and were not modulated by pubertal maturation or levels of sex hormones.

In **Study II**, we investigated whether the female own-gender bias in face recognition could be explained by women encoding female faces more elaborately than male faces. The results showed that divided attention at encoding, which may hamper elaborate encoding, did not reduce the magnitude of women's own-gender bias, but attenuated women's advantage over men in memory for female faces.

Whether the gender of a face influenced men and women's visual attention and memory for own- and other-race faces, and whether viewing time influenced the own-race bias, was investigated in **Study III**. Women displayed an own-gender bias, irrespective of face ethnicity. More importantly, own-race female faces were viewed longer and were better recognized than other-race female faces, whereas these differences were smaller for male faces. However, differences in viewing time could not account for the magnified own-race bias found for female faces.

The aim of **Study IV** was to assess whether women's brain activity was higher for female than male faces in fusiform and inferior occipital gyri during incidental encoding of faces, and whether there was a relation between brain activity in fusiform gyri and the gender bias in face recognition. Results from this event-related fMRI study showed that women recognized more female than male faces, and that their brain activity during encoding was higher for female than for male faces in fusiform and inferior occipital gyri. Differential activity in left fusiform to female versus male faces was related to differences in memory for female and male faces.

Taken together, the results of this thesis suggest that neither sex differences in cognitive abilities nor the female own-gender bias result from pubertal maturation or its associated changes in levels of sex hormones. Instead, the reasons for these differences should possibly be sought after earlier in development. With regard to the female own-gender bias, results suggest that this effect is reliable, not affected by divided attention at encoding, associated with increased brain activation in regions specifically involved in face processing, and potentially a result of perceptual expertise.

LIST OF PUBLICATIONS

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LIST OF ABBREVIATIONS

BOLD	Blood oxygen level-dependent (response)
fMRI	Functional magnetic resonance imaging
ROI	Region of interest
FFG	Fusiform gyrus
FFA	Fusiform face area
IOG	Inferior occipital gyrus
OFA	Occipital face area
STS	Superior temporal sulcus
T	Testosterone
E ₂	Estradiol
SHBG	Sex hormone-binding globulin
ISI	Inter-stimulus interval
RT	Reaction time
<i>d</i>	Cohen's <i>d</i> (standardized effect size)
<i>d'</i>	Discrimination sensitivity
ANOVA	Analysis of variance
MANOVA	Multivariate analysis of variance

1 INTRODUCTION

“The chief distinction in the intellectual powers of the two sexes is shewn [shown] by man attaining to a higher eminence, in whatever he takes up, than woman can attain - whether requiring deep thought, reason, or imagination, or merely the use of the senses and hands. If two lists were made of the most eminent men and women in poetry, painting, sculpture, music, - comprising composition and performance, history, science, and philosophy, with half-a-dozen names under each subject, the two lists would not bear comparison.” (Darwin, 1871, p. 327).

“The three main conclusions that the investigation seems to justify are as follows:

- 1. The women excel the men noticeably in either immediate or delayed memory work.*
- 2. The men excel the women, but to a less degree, in reason work.*
- 3. Both sexes prefer memory work, but a greater relative number of men show a willingness to do reason work in lieu of memory work.” (Gates, 1917, p.146)*

The study of behavioral sex differences has a long history (e.g., Darwin, 1871), being controversial from the very beginning. Men were seen as more intelligent than women, as there were few – if any – acknowledged female geniuses in most areas of science and arts (Darwin, 1871; Lombroso, 1895). Darwin (1871) argued that men’s intellectual advantage was a result of part sexual selection, part natural selection. On the other hand, he did not consider that throughout ancient and modern times, women have not had access to higher education or more complex occupations, suggesting that the wealth of male geniuses was not reflecting true sex differences in intellectual abilities.

With large-scale studies of intelligence, and as girls and women gained access to higher education, it was noted in the beginning of the 20th century that there were generally no sex differences in overall scores on intelligence tests (for a review, see Thompson Woolley, 1914). This is also the case today, but it should be noted that even though there are overall no sex differences on intelligence tests, there are sex differences on certain tests of specific cognitive abilities. In addition, the magnitudes and even the direction of cognitive sex differences are to some extent shaped by cultural factors – such as females’ access to education (e.g., Herlitz & Kabir, 2006; Hoffman, Gneezy, & List, 2011).

Few research areas have been as questioned as the study of sex differences in cognitive abilities. Some have argued that the study of sex differences may be harmful, as these studies magnify differences between men and women instead of pointing out that there are no sex differences in a number of cognitive abilities, suggesting that women and men are more similar than they are different (Hyde, 2005). On the other hand, it has been argued that the study of cognitive sex differences is of interest in itself, as this may further our understanding of individual differences in these particular cognitive skills and how these abilities are organized (Kimura, 1999).

Regardless of one’s opinion on the study of sex differences, there are numerous studies, conducted across different cohorts and cultures, showing that females excel on some cognitive tasks and males on others (e.g., de Frias, Nilsson, & Herlitz, 2006; Owen &

Lynn, 1993). It is not clear why there are cognitive sex differences, but there are plenty of hypotheses (e.g., Halpern, 2012; Maccoby & Jacklin, 1974). In the present thesis, I will address some of these hypotheses (Section 1.1), with a special focus on face recognition memory and the gender bias in memory for faces (Section 1.3).

The magnitudes of cognitive sex differences range from small to large, much depending on the ability assessed. Magnitudes of differences are typically expressed in standard deviation units, Cohen's d , which conventionally have been classified according to their size as small ($|.20| \leq d \leq |.49|$), medium ($|.50| \leq d \leq |.79|$), or large ($d \geq |.80|$; Cohen, 1988). A small effect, such as $d = 0.20$, indicates that the overlap between the two performance distributions is approximately 85%; for a medium sized effect, $d = 0.50$, the overlap is 67%, and for a large effect size, $d = 0.80$, 53% (Cohen, 1988). Note that a small effect size does not necessarily mean that it is unimportant or of less interest than a large effect size (for a discussion, see Prentice & Miller, 1992). Throughout the thesis, whenever an effect size of a sex difference is reported, a positive value refers to a female advantage, and a negative value indicates a male advantage.

Finally, I would like to comment on my use of certain terms in this thesis. When referring to a difference in performance between males and females, I use the term sex, and when referring to whether a face is female or male, I use the term gender. I also use the term "own-gender bias" when referring to better memory for faces of one's own sex compared to memory for faces of the other sex. Sex and gender have originally been used to mark whether one holds that differences found in performance between females and males are biologically based (sex) or socially based (gender), but no such meaning is inherent in my use of these terms. In a similar vein, I tend to use the terms race and ethnicity interchangeably throughout this thesis, even though these terms do not have the same meaning.

1.1 SEX DIFFERENCES IN COGNITIVE ABILITIES

Two of the most well-studied cognitive abilities typically showing sex differences are found in the verbal and the spatial domains. Another cognitive ability showing sex differences is episodic memory, and in particular memory for faces, which is a special focus of the present thesis. Before reviewing face recognition memory in Section 1.2, I will present an overview of sex differences in verbal abilities, spatial abilities, and in episodic memory for different materials.

1.1.1 Verbal abilities

Girls and women typically excel over boys and men in performance on some, but not all, verbal tasks. These tasks assess various forms of using and understanding language. Generally, a female advantage has been found on phonemic verbal fluency tasks, requiring a rapid generation of words beginning with a certain letter (e.g., "A", $d = .33$; Hyde & Linn, 1988; see also Bolla, Lindgren, Bonaccorsy, & Bleecker, 1990; Herlitz, Airaksinen, & Nordström, 1999; Levin, Culhane, Hartmann, & Evankovich, 1991), whereas there are typically no sex differences on semantic fluency tasks, in which as many words within a category are to be generated (e.g., "animals", Weiss et al., 2006; but see Halari et al., 2005). Maccoby and Jacklin (1974) suggested that boys and girls perform similarly on most verbal tasks, but after age 11, the sex difference becomes

intensified in for instance verbal production. In line with this notion, Levin et al. (1991) found that girls' advantage on phonetic (henceforth referred to as verbal) fluency tasks was present between ages 9-15, but there was no sex difference between ages 7-8. Similarly, Sincoff and Sternberg (1988) found that girls' advantage over boys in verbal fluency was larger in 11-year-olds than in 8-year-olds. The female advantage on verbal production tasks has been confirmed across various countries (e.g., Mann, Sasanuma, Sakuma, & Masaki, 1990). Finally, there are typically no sex differences on vocabulary tasks (e.g., Hyde & Linn, 1988; Levine, Huttenlocher, Taylor, & Langrock, 1999).

1.1.2 Spatial abilities

Males typically excel over females in tasks tapping spatial abilities (for meta-analyses, see Linn & Petersen, 1985; Voyer, Voyer, & Bryden, 1995). Spatial abilities have been separated into three subcomponents: spatial perception (rod and frame test, water level test), spatial visualization (e.g., block design, paper folding), and mental rotation (Linn & Petersen, 1985). Even though a male advantage has been found on spatial perception ($d = -0.44$), and a smaller advantage on spatial visualization tasks ($d = -0.19$), the largest sex difference is typically found on mental rotation tasks ($d = -0.56$; Voyer et al., 1995). In a typical mental rotation task, a target figure consisting of cubes is presented. Rotated versions of this figure are presented among other similar figures, and the goal is to determine which of the figures that is the same as the target. Assumedly, this type of task requires the ability to imagine how an object would look like if rotated in space.

Some findings indicate that sex differences in spatial abilities emerge during puberty (e.g., Maccoby & Jacklin, 1974; Voyer et al., 1995); others have found that the male advantage on spatial perception and mental rotation is present during early childhood (Levine et al., 1999; Linn & Petersen, 1985; Liu & Lynn, 2011). There are also studies that have used habituation paradigms to assess whether there are early sex differences in the ability to recognize a rotated object. In a typical habituation paradigm, the infant is familiarized with a material. To test recognition, the familiar material is paired with an unfamiliar material. If the infant prefers to view the novel compared to the familiar material, this is taken to indicate that the infant recognized the familiarized material. Interestingly, there were sex differences in viewing preferences, showing that 3- to 5-month-old boys, but not girls, preferred to view novel objects compared to habituated but rotated objects (Moore & Johnson, 2008; Quinn & Liben, 2008). Finally, a male advantage on mental rotation tasks has been confirmed in a wide variety of cultural contexts (e.g., Janssen & Geiser, 2012; Mann et al., 1990; Owen & Lynn, 1993).

1.1.3 Episodic memory

Episodic memory refers to the ability to remember a personal experience (what), its occurrence in subjectively experienced time (when), and the place in which it occurred (where; Tulving, 2002). Episodic memory tasks comprise learning of a material and a memory test. The encoding can be either intentional (the participant is instructed that a memory test will follow) or incidental (a surprise memory test is completed). An unrelated task is usually performed between learning and the memory test to prevent repetition of the material. After this interval, which can last from a couple of minutes to days or months, a memory test is completed, which varies in difficulty depending on

the amount of support provided. The most difficult task is free recall, as no support is given. Cued recall gives some support; for instance, if word pairs are encoded, one word from each pair can be used as a cue for recall of the second word. Most support is given in recognition tasks, in which the old material is presented intermixed with a new material, and the task is to indicate whether each item is recognized or not.

The direction and magnitude of sex differences in episodic memory depend largely on the type of material used (for a review, see Herlitz & Rehnman, 2008). Females often perform at a higher level than males when the material to be recalled or recognized is verbal (e.g., Herlitz, Nilsson, & Bäckman, 1997; Kramer, Delis, Kaplan, O'Donnell, & Prifitera, 1997), whereas a male advantage has been found for recall of visuospatial information, such as shading of a figure (Lewin, Wolgers, & Herlitz, 2001). Cross-sectional studies of children, adolescents, and young adults have confirmed that the female advantage is present on verbal episodic memory tasks from at least age 5 (e.g., Gur et al., 2012; Keith, Reynolds, Roberts, Winter, & Austin, 2011; Lowe, Mayfield, & Reynolds, 2003) and into old age (90 years, de Frias et al., 2006; 70-100 years, Gerstorf, Herlitz, & Smith, 2006). Interestingly, women also show an advantage in memory for object locations (for a review and meta-analysis, see Voyer, Postma, Brake, & Imperato-McGinley, 2007), which is somewhat surprising given that the nature of this task is arguably more spatial. Moreover, women excel over men in odor recognition memory (Larsson, Lövdén, & Nilsson, 2003; see also Choudhury, Moberg, & Doty, 2003; Doty & Kerr, 2005). Girls and women also perform at a higher level than boys and men on face recognition memory tasks (e.g., Bengner et al., 2006; Gur et al., 2012; Rehnman & Herlitz, 2006; Rehnman & Herlitz, 2007). The sex difference in memory for faces is a special focus of this dissertation and is reviewed in depth in Section 1.3.

1.1.4 A comment: Cultural influences

Even though I have stated that sex differences in some abilities are well established, as they have been replicated across different samples, ages, and countries, it should be noted that some of these group differences may depend on the degree of gender equality in the society (as assessed by girls' and women's access to education, more qualified occupations, childcare opportunities, etc.). Herlitz and Kabir (2006) compared sex differences on subtasks of the Mini-Mental State Examination in samples of illiterate and literate Bangladeshi participants and Swedish participants. What is striking with this study is that women performed less well than men in the illiterate Bangladeshi group on almost all tasks, and there was no sex difference in free recall. However, in the literate Bangladeshi group, sex differences favored men and women as seen in many Western societies. Another example comes from a cross-sectional study of boys and girls between ages 5-16 in Colombia and Mexico (Ardila, Rosselli, Matute, & Inozemtseva, 2011). Even though there was a male advantage on one of the spatial tasks, boys' performance was higher than girls' in language comprehension and there was no sex difference in recall of words or figures. Yet another example comes from the PISA study, investigating 15-year-old students' math and reading abilities in more than 40 countries (Guiso, Monte, Sapienza, & Zingales, 2008). Boys' advantage over girls in math was very small or non-existent in countries with higher gender equality, whereas girls' advantage over boys in reading remained and became larger in countries with higher gender equality. These studies indicate that education, culture, and/or gender equality modulate the magnitude of cognitive sex differences.

1.1.5 Explanations of sex differences in cognitive abilities

Broadly speaking, explanations of cognitive sex differences can be separated into two main areas – social and biological. Social explanations generally assume that most behavioral sex differences are a result of differential socialization of females and males (e.g., Bem, 1983), which for instance could influence their play preferences in childhood, later educational and occupational choices, and in turn cognitive sex differences. In contrast, biological explanations share the notion that biological differences, such as in levels of sex hormones and in turn, their influence on the brain, may contribute to behavioral sex differences (e.g., Berenbaum & Beltz, 2011; Hampson, 1995). This perspective typically holds that individual experience and evolution shape these differences (Kimura, 1999). However, it should be noted that no clear separation between biology and culture/environment can be made, as any given biological influence on cognitive abilities must be developed through interactions between the individual and the environment, and the environment can affect the expression of genes (Gottlieb, 1998).

Explanations of cognitive sex differences can be separated based on their level of explanation. The social explanations mentioned earlier concern societal and parental influences. Some biological explanations are mainly occupied with hemispheric organization of the brain or regional brain volumes, others with hormonal and/or genetic influences on the organization of the brain and neural signaling during different stages of development. Even though focus may be put on different levels, most biological explanations eventually arrive at the genetic and/or the cellular level (e.g., Geschwind & Galaburda, 1985a-c; Hines, 2010). To illustrate this hierarchy of explanation levels, I will start off with a discussion of a common approach to explain sex differences in episodic memory. This will be followed by a summary of two explanations of importance for the present thesis, which focus on puberty and the relation between endogenous sex hormones and individual differences in cognitive performance.

1.1.5.1 *Explaining sex differences with sex differences*

To better understand why a sex difference may be found in a particular cognitive ability, it has been of interest to assess whether sex differences in a certain cognitive ability may drive another. For instance, as performance on many episodic memory tasks can be improved by verbalization of the material during encoding, it has been suggested that women's higher skill in verbal processing or verbal production may explain sex differences favoring women in odor memory (Larsson et al., 2003), face recognition memory (Lewin & Herlitz, 2002), object location memory (Lejbak, Vrbancic, & Crossley, 2009), memory for activities (Herlitz et al., 1997), free recall and recognition of common objects (Herlitz et al., 1999) and words (Herlitz et al., 1999; Herlitz et al., 1997; Larsson et al., 2003). Interestingly, women's advantage over men remained on all episodic memory tasks mentioned above when verbal processing skills were controlled for – apart from two: women's advantage in memory for odors and verbal episodic memory (Herlitz et al., 1999; Larsson et al., 2003; but see also Herlitz et al., 1997). Similarly, as women typically perform better than men on tasks assessing memory for words, odors, faces, objects, and object locations, it has been suggested

that women have a slight general advantage in episodic memory compared to men (Herlitz & Rehnman, 2008). However, when explaining one sex difference by another, the issue remains - why do we observe a sex difference in the first place?

1.1.5.2 Sex hormones – sex differences?

There are several biological explanations of cognitive sex differences (for reviews, see Collaer & Hines, 1995; Halpern, 2012; Hines, 2004). Most of these hold, in one way or another, that sex hormones influence the organization of the brain, and in turn, behavior. It is beyond the scope of the present thesis to review them all. Here, I will focus on studies of sex hormones and pubertal development in humans, and the following two hypotheses: (1) onset of puberty magnifies cognitive sex differences (e.g., Voyer et al., 1995), and (2) individual differences in endogenous levels of sex hormones influence cognitive abilities (e.g., Kimura & Hampson, 1994; Nyborg, 1983). Many of these ideas originate from experimental animal work, showing that manipulated levels of sex steroids during prenatal and the pubertal phases of development organize the brain, social and sexual behaviors, and performance on various cognitive tasks (for a review, see Sisk & Zehr, 2005). Before reviewing the role of puberty and sex hormones in cognitive sex differences, I will provide a brief overview of physical development during puberty.

The prepubertal stage, adrenarche, typically begins between ages 6-9 in girls and approximately one year later in boys with an increase of adrenal androgen production, but this surge of weak androgens (e.g., dehydroepiandrosterone – DHEA) occurs without changes in secondary sex characteristics (e.g., Cameron, 2004). The second stage of pubertal development, gonadarche, begins approximately two years after adrenarche and is initiated by the activation of the hypothalamic-pituitary-gonadal axis (Reiter & Grumbach, 1982). Increased production of gonadotropin releasing hormone in the hypothalamic neurons stimulates the production of luteinizing hormone and follicle-stimulating hormone in the pituitary, which initiates the production of sex hormones in the gonads – androgens (e.g., testosterone [T]) and estrogens (e.g., estradiol [E₂], progesterone). Thus, the primary sexual characteristics mature (ovaries, testes) during gonadarche and the secondary sex characteristics become fully developed (e.g., pubic hair, breasts, genitals) as a result of the increased levels of endogenous sex hormones. The final stage of puberty is the onset of menses (menarche) for girls, and the onset of emissions for boys (spermarche; Dorn, Dahl, Woodward, & Biro, 2006). After puberty and during the major part of adulthood, levels of sex hormones differ markedly between men and women, even though the “male” androgens and the “female” estrogens are present in both sexes.

As males and females’ exposure to endogenous sex hormones differ throughout the life span, it has been of interest to determine whether cognitive sex differences may be explained by these hormonal sex differences. Broadly speaking, there are two routes by which hormones are thought to influence the brain, and in turn behavior. Based on their work on guinea pigs, Phoenix, Goy, Gerall, and Young (1959, as reviewed in Wallen, 2009) proposed that prenatal levels of testosterone influence the expression of sex-specific mating behaviors in adult animals. The effects of sex hormones were separated into organizational effects occurring early, having a permanent effect on the brain, and

activational effects occurring later in development, which are short-term hormonal influences acting on existing neural systems (for an overview, see Goy & McEwen, 2007). Even though sex differences in prenatal and early postnatal exposure to T are two periods of particular interest for assessing potential organizational effects (e.g., Hines, 2010), puberty has been proposed as an additional important period (Sisk & Zehr, 2005). Gonadal steroids have been shown to affect numerous neuronal processes, for instance the formation and elimination of synapses, cell birth, cell death, and neurotransmitter receptor expression, and there are plenty of androgen and estrogen receptors distributed in other brain areas than hypothalamus (for a review, see Cameron, 2004). In addition, these hormones have been shown to act on brain regions involved in cognitive functions, including hippocampus, amygdala, and striatum (for a review, see Gillies & McArthur, 2010). For instance, animal studies have shown that estrogen interacts with dopamine transmission in the striatum (Becker, 1999), and there are findings indicating that in humans, genetic markers of COMT enzyme activity in the prefrontal cortex interact with the natural fluctuation of estrogen during the menstrual cycle, influencing spatial working memory performance as well as prefrontal brain activity while performing the task (Jacobs & D'Esposito, 2011).

1.1.5.3 Puberty and sex differences in cognitive abilities

Waber (1976, 1977) proposed maturation rate to be important for the development of cognitive functions, and suggested that sex differences in certain abilities (verbal, spatial) are a result of most girls maturing earlier than boys, with differential lateralization of the brain as the proposed mechanism. Waber suggested that earlier maturing individuals may be less lateralized during verbal (speech) processing than later maturers, which would improve early maturers' performance on verbal tasks, whereas their bilateral lateralization would interfere with spatial processing. Thus, later maturing individuals would tend to be more lateralized than earlier maturing individuals, in turn facilitating performance on spatial tasks compared to verbal task performance. Generally, there has not been consistent support for the idea that early maturing individuals have an advantage on verbal compared to spatial tasks, or the reversed pattern for later maturers (for a review and meta-analysis, see Newcombe & Dubas, 1987).

Another suggestion is that sex differences in cognitive abilities, particularly in spatial abilities but also in verbal abilities, are first observed or magnified during puberty (Maccoby & Jacklin, 1974; McGee, 1979; Voyer et al., 1995), which may suggest a role of pubertal sex hormones. Similarly, as studies of rodents indicate that sex hormones during puberty organize behavior in a sex-dependent manner, it has been suggested that pubertal hormones may also organize cognitive functions in humans (Sisk & Zehr, 2005). The increased levels of sex hormones during puberty may influence signaling in and/or development of task-relevant brain regions, particularly if these regions contain androgen or estrogen receptors. As an example, it has been shown that in 12-year-old girls and 13-year-old-boys, sex differences in gray matter volume in some regions of the medial temporal lobe (right hippocampus, amygdala) were larger for individuals with more advanced puberty and higher levels of testosterone (Bramen et al., 2011). At present, there are some studies, reviews, and meta-analyses suggesting that sex differences in verbal fluency and mental rotations are smaller before puberty

than after (e.g., Levin et al., 1991; Maccoby & Jacklin, 1974; Voyer et al., 1995). On the other hand, there are findings indicating that sex differences on these tasks are found well before puberty (Levine et al., 1999; Sincoff & Sternberg, 1988).

In sum, sex differences in cognitive abilities seem to be present early, especially in verbal episodic memory and mental rotations, but it is not clear whether these sex differences indeed are magnified during puberty or not. In Study I, we tested whether cognitive sex differences became larger throughout ages 12-14, and whether sex differences were larger between individuals with higher levels of sex hormones (indicating more advanced puberty) or more advanced puberty (as indicated by self-ratings of pubertal development).

1.1.5.4 Endogenous sex hormone levels and cognitive performance

In humans, the relation between sex hormones and cognition is typically assessed by studying inter- or intra-individual differences in levels of endogenous sex hormones. Another approach, albeit less common, is to investigate effects of administration/suppression of endogenous sex hormones on cognitive performance.

There are various hypotheses regarding the relation between sex hormones and performance on different cognitive tasks (for an overview of sex hormones and spatial abilities, see Davison & Susman, 2001). For instance, it has been suggested that there is a range of hormone levels that gives an optimal performance on spatial tasks. As androgens can be aromatized to estradiol, Nyborg (1983) proposed that females have more than optimal levels of estradiol for spatial performance, and males lower than optimal levels. Thus, a positive relation between levels of estradiol and spatial performance would be expected for males, and a negative relation for females. Overall, there are few studies showing a relation between levels of estradiol and performance on spatial tasks, as a positive relation has been observed for women, but no relation for men (Janowsky, Chavez, Zamboni, & Orwoll, 1998), and a positive relation for boys aged 10-14 years but no relation for girls aged 9-14 years (Davison & Susman, 2001). Similarly, a non-linear relation between T and spatial performance has been proposed, which has received some support (Gouchie & Kimura, 1991; but see Halari et al., 2005).

Moreover, there are variations of this idea, holding that the relation between levels of testosterone and spatial performance is linear (see Davison & Susman, 2001). Indeed, there are findings of a positive relation between levels of testosterone and performance on spatial tasks in boys and men (Burkitt, Widman, & Saucier, 2007; Davison & Susman, 2001; Hassler, 1992; Hooven, Chabris, Ellison, & Kosslyn, 2004; Silverman, Kastuk, Choi, & Phillips, 1999; Thilers, MacDonald, & Herlitz, 2006), but there are also studies reporting a negative relation (Moffat & Hampson, 1996) or no relations for men or boys (Halari et al., 2005; Hassler, 1992; Hassler, Gupta, & Wollmann, 1992; Janowsky et al., 1998; Kampen & Sherwin, 1996; Puts et al., 2010; Yonker, Eriksson, Nilsson, & Herlitz, 2006). For females, there are studies showing a positive (Moffat & Hampson, 1996) or no relation between levels of testosterone and spatial performance (Davison & Susman, 2001; Halari et al., 2005; Hassler, 1992; Hassler et al., 1992; Janowsky et al., 1998; Puts et al., 2010).

For verbal fluency, no consistent relations have been found between performance and levels of estradiol or testosterone for either women or men (Christiansen & Knusmann, 1987; Halari et al., 2005; Hassler et al., 1992; Janowsky et al., 1998; Moffat & Hampson, 1996; Thilers et al., 2006).

There are few studies of the relation between individual differences in episodic memory performance and sex hormone levels in children, adolescents, or young adults. Most studies have assessed these relations in perimenopausal and/or postmenopausal women, mainly with regard to effects of hormone replacement therapy, and in elderly adults (but see Janowsky et al., 1998). As for the findings reported above for performance on spatial tasks and verbal fluency, there are studies showing a positive relation (Hogervorst, De Jager, Budge, & Smith, 2004; Wolf & Kirschbaum, 2002), a negative relation (Tuomisto, Salo, Saarinen, Kalleinen, & Polo-Kantola, 2012), or no relation (Luetters et al., 2007) between verbal episodic memory and estradiol levels in middle-aged and/or older women and men. Few studies have shown a relation between testosterone and verbal episodic memory performance in elderly men (for a review, see Warren, Serby, & Roane, 2008).

Taken together, the support for a relation between endogenous sex hormone levels and cognitive performance across individuals is mixed. There are findings showing positive, negative, and no associations between sex hormones and cognitive performance, although most studies have assessed spatial abilities, and particularly mental rotations. Moreover, there are few studies on young adolescents, as most studies on the relation between sex hormones and cognitive performance are based on adults. In Study I, potential relations between individual differences in sex hormones and performance on cognitive tests typically yielding sex differences were assessed in a sample of young adolescents (ages 12-14).

1.2 FACE RECOGNITION

Faces are a very important type of social stimulus for many species, particularly for primates, but also for other mammals with complex social structures (for a review, see Leopold & Rhodes, 2010). For humans, faces are the most important social stimulus there is, as face-to-face communication from birth is the first and the major manner in which we socially communicate with each other. Faces provide a rich source of information, which can be separated into two major components: face traits and face states (e.g., Pascalis et al., 2011). Face traits are the stable characteristics of a face, such as species, sex, age, ethnicity, aesthetics (attractivity), and the individual's identity. Face states are the dynamic facial movements expressed by the individual, such as speech, emotion, and direction of gaze.

Another important distinction between facial information that has been made is between configural (the spatial relation between facial features) and featural information (eyes, nose, mouth, hair, jawline; Maurer, Le Grand, & Mondloch, 2002). Compared to other objects, faces seem to be processed in a more configural or holistic manner, that is, recognition of faces is based on their configurations of features rather than on their individual features (for a review, see Maurer et al., 2002); I will return to

this topic in the next section. Various models have been put forward to describe the process of recognizing a familiar face. Common for these models is that there are multiple stages, beginning with that the face is encoded, then matched with a stored representation of the face, its associated semantic information, and finally, the name may be recalled (e.g., Bruce & Young, 1986). Valentine (1991) proposed a multidimensional space model, suggesting that unfamiliar faces are encoded as vectors in this space, in relation to their deviation from a norm face (an “average” face representation). This means that typical faces would be distributed close to the origin, and distinctive faces would be located further away from the origin.

Throughout this thesis, I use the terms face recognition and face recognition memory interchangeably when referring to studies assessing memory for faces using episodic memory tasks (e.g., yes/no recognition tests, longer interval between encoding and test, e.g., 5-10 minutes). Other types of tasks assessing other aspects of face processing are also sometimes referred to as recognition tasks in the literature, such as tasks assessing identification of emotional expressions. This has led to misinterpretations of results, for instance that women’s advantage over men in memory for faces could be explained by women’s advantage in emotion identification (Halpern, 2012). Therefore, I refer to face recognition tasks that have a very short interval between each target and test face (a few ms or sec) as face identification or discrimination tasks, as these are not tests of episodic memory for faces. Finally, I would also like to highlight that most studies I refer to used “neutral” faces, that is, faces that do not express any particular emotion, and I will explicitly state when faces displaying emotional expressions were used.

1.2.1 Is face processing special?

There is plenty of evidence supporting the notion that face processing is functionally separated from processing of other objects. Patients with acquired prosopagnosia (“face blindness”) have typically neural damage in either bilateral or right ventral temporal and/or occipital cortex, resulting in impaired face recognition (e.g., Farah, Rabinowitz, Quinn, & Liu, 2000). Importantly, patients with prosopagnosia do not necessarily show impaired recognition of other objects, and some patients with object agnosia can recognize faces (e.g., Moscovitch, Winocur, & Behrmann, 1997). Studies using various brain imaging methods, such as positron emission tomography (PET) and functional magnetic resonance imaging (fMRI), have confirmed that some areas of the brain are specifically involved in face processing. fMRI of blood oxygen level-dependent (BOLD) responses measures indirectly neural responses in various brain regions during performance of cognitive tasks. There are now plenty of studies in adults that have confirmed that faces compared to other objects consistently activate specific regions within especially the fusiform (FFG) and inferior occipital gyri (IOG; Haxby et al., 1996; Kanwisher, McDermott, & Chun, 1997; Kanwisher & Yovel, 2006).

Haxby, Hoffman, and Gobbini (2000) suggested that the core system for face processing comprised the following areas: the occipital face area (OFA), located in the mid/inferior occipital cortex (IOG), involved in the early visual analysis of face parts (for a review, see Pitcher, Walsh, & Duchaine, 2011); the fusiform face area (FFA), located in the FFG, engaged in individuation or holistic processing of faces (Rhodes, Byatt, Michie, & Puce, 2004; Schiltz, Dricot, Goebel, & Rossion, 2010); the superior

temporal sulcus (STS), mainly involved in processing of facial movement, such as mouth movement (Pelphrey, Morris, Michelich, Allison, & McCarthy, 2005). Studies assessing functional and effective connectivity between these core regions have generally confirmed that this is a reasonable neural model of the face processing network (Cohen Kadosh, Cohen Kadosh, Dick, & Johnson, 2011; Fairhall & Ishai, 2007). The selectivity of FFA and other regions for faces compared to other objects has typically been operationalized as the number of activated voxels and/or the average blood oxygen level-dependent (BOLD) response in the whole ROI and/or the magnitude of peak voxel response in this ROI to faces compared to common objects (e.g., Furl, Garrido, Dolan, Driver, & Duchaine, 2011; Kanwisher et al., 1997).

In addition to the core system, Haxby et al. (2000) proposed an extended system that includes among other regions the amygdala, insula, the limbic system (processing of facial expressions), and the anterior temporal lobe (processing of semantic information related to the individual). However, there are different views on which regions to include in the extended network. As an example, Ishai (2008) included the amygdala, orbitofrontal cortex, and the inferior frontal gyrus.

There are several behavioral findings indicating that faces are processed differently from other objects. To begin with, face identification and recognition is disproportionately impaired by inversion (the “inversion effect”; Yin, 1969). Thus, if faces are presented up-side down, encoding and recognition becomes more difficult, whereas encoding and recognition of other types of stimuli, such as houses or landscapes, are not as sensitive to inversion. Moreover, the importance of configural processing in face identification has been shown by a paradigm that use composite faces. If the top half of a face is combined with the lower half of another individual’s face, this composite face is typically perceived as a new individual, and identification of the individual depicted in the top half is slower and less accurate when the two halves are aligned compared to when they are misaligned horizontally (the “composite effect”; Young, Hellawell, & Hay, 1987). In addition, facial features are better identified when presented in a face than when presented in isolation (the “part-whole effect”; Tanaka & Farah, 1993), and changes to the facial configuration impair memory for facial features (Tanaka & Sengco, 1997). Thus, human faces seem to be preferentially processed as wholes, and manipulations that interfere with holistic processing typically impair face identification and recognition, but not recognition of other types of objects.

Another line of evidence comes from studies of infants’ and children’s face perception and recognition. Newborn infants preferentially attend to face-like configurations compared to random configurations of facial parts (for a review, see Johnson, 2005). However, there are also many findings suggesting that experiences shape facial preferences during infancy. For example, a few days after birth, infants prefer to attend to their mother’s face compared an unfamiliar female adult (Bushnell, Sai, & Mullin, 1989). Three-month-old infants are typically exposed to more female than male faces (Rennels & Davis, 2008), and mother-reared infants prefer to look at a novel female over a novel male face, whereas infants who primarily had been raised by their father prefer male compared to female faces (Quinn, Yahr, Kuhn, Slater, & Pascalis, 2002). Similarly, Chinese and Caucasian infants prefer to look at own-race compared to other-

race faces (Kelly et al., 2005; Kelly et al., 2007). In addition, there are findings indicating a sensitive period for learning faces of different species and ethnicities in infancy. Pascalis, de Haan and Nelson (2002) found that 6-month-old infants could discriminate between previously seen and novel monkey faces. Moreover, children who had had experience with monkey faces during ages 6-9 months could recognize monkey faces when they were 9 months old, whereas no novelty preferences were found for children without previous experience (Pascalis et al., 2005). Similarly, infants aged 8-10 months who received brief daily other-race face experience during three weeks could discriminate between other-race faces after this period (Anzures et al., 2012). These findings indicate that even though infants initially show a preference for facial configurations, early visual preferences and the ability to discriminate between faces are shaped by the infants' experiences.

Throughout childhood and adolescence, face recognition memory improves steadily (e.g., Gur et al., 2012), and from about age 5, children show holistic processing of faces (Crookes & McKone, 2009; Tanaka, Kay, Grinnell, Stansfield, & Szechter, 1998). However, the preferential BOLD response in FFG to faces seems to emerge later. Findings from fMRI studies indicate that 5- to 8-year-old children do not show specificity in FFG for faces compared to other objects as older children and adults do (Scherf, Behrmann, Humphreys, & Luna, 2007). The activated volume of the right FFA has been shown to be larger in adults than in children (Golarai et al., 2007), and in adults compared to adolescents (Golarai, Liberman, Yoon, & Grill-Spector, 2010). Moreover, children do not show a similar strength in effective connectivity between FFG, IOG, and STS as adults do in response to different task demands during face processing (Cohen Kadosh et al., 2011).

It is generally agreed upon that adults are face experts and experience shapes the ability to process faces, but there are different views on how this special ability develops (for a review, see Pascalis et al., 2011): either from an innate specialized face-processing mechanism (the modularity hypothesis; Kanwisher, 2000) or from the extreme amount of exposure to faces (a general learning effect; Nelson, 2001). The modularity hypothesis suggests that humans are born with a special neural module that is specifically dedicated to face processing, and to face processing only. This idea is supported by animal work, showing that even if no early facial experience was provided during the first 6-24 months, Japanese macaques showed a visual preference for both human and monkey faces to non-face objects, and could discriminate between new and old faces (Sugita, 2008).

However, there are many findings suggesting that faces may rather be a category of objects that we have a large amount of experience with, and in turn, regions of the core system "dedicated" to faces may also be activated by objects-of-expertise. This has been supported by studies on expertise with non-face materials, such as chess experts (e.g., Bilalić, Langner, Ulrich, & Grodd, 2011; Gauthier, Skudlarski, Gore, & Anderson, 2000), as well as training studies using an artificial species (Gauthier & Tarr, 1997, 2002). There are also behavioral findings suggesting that processing of objects-of-expertise to some extent resembles face processing, as inversion effects are also found for experts on their objects-of-expertise (e.g., Diamond & Carey, 1986).

A middle-way view on the development of face processing is the interactive specialization theory, which holds that infants are born with a predisposition to attend specifically to face configurations (for a review of this framework, see Johnson, 2011). This is accomplished by a subcortical route consisting of the amygdala, pulvinar, and superior colliculus, activated by low spatial frequency information in faces. This information comes mainly from the facial configuration. In turn, faces filtered to contain a range of low spatial frequencies look coarse and blurred (for an example, see Vuilleumier, Armony, Driver, & Dolan, 2003).

The idea is that the subcortical route is activated when faces are detected, especially in the periphery of vision, which would enable infants to orient their gaze towards objects (i.e., faces with a direct view) appropriate for social interaction. Moreover, this route assumedly projects onto cortical areas, which may put anatomical and functional constraints on particular areas (the core face network) that increasingly become tuned to faces throughout development. In short, this theory has great appeal as it can explain a large part of empirical findings, including the orienting response to faces observed in newborn infants (Johnson, 2011).

1.3 INDIVIDUAL DIFFERENCES IN FACE RECOGNITION

Even though I earlier alluded to that all adults are experts in face processing, this is naturally an oversimplification. Patients with developmental prosopagnosia have great difficulties in recognizing faces, even faces belonging to highly familiar persons, but no known brain lesions. Some have argued that developmental prosopagnosia may be seen as the lower end of a continuum of the ability to recognize and discriminate between faces (Furl et al., 2011). In turn, BOLD responses in FFA may be linked to individual differences in face recognition memory performance, that is, degree of face-related activation in this brain region may be related to performance on face memory tasks. Furl and colleagues (2011) found that a higher BOLD response in FFA predicted better performance on face recognition tasks in a sample of patients with developmental prosopagnosics and controls. In a similar vein, at the higher end of the distribution of skills in face processing and recognition are individuals who seem unable to ever forget a face - “super-recognizers” (Russell, Duchaine, & Nakayama, 2009). Russell et al. (2009) assessed the performance of three women and one man, reporting that they were exceptionally good at recognizing others. These “super-recognizers” performed well above the range of controls on face memory tasks, as well as on a perceptual face discrimination task, and interestingly, showed a larger face inversion effect than controls. Controls, in turn, showed a larger face inversion effect than patients with developmental prosopagnosia (Russell et al., 2009). Other studies of individual differences in face recognition have, for instance, shown that individuals classified as high in empathy or extraversion remember more faces than individuals categorized as low in empathy or extraversion (e.g., Bate, Parris, Haslam, & Kay, 2010; Li et al., 2010). However, one basic difference is typically found between females and males – females typically perform higher than males on face processing and recognition memory tasks.

1.3.1 Sex differences in face perception

To begin with, sex differences in infants' attention to faces have been observed. In a sample of newborn infants, who were approximately 37 hours old, girls attended more to a female face than young infant boys, whereas boys attended more to a mechanical object (i.e., a moving mobile; Connellan, Baron-Cohen, Wheelwright, Batki, & Ahluwalia, 2000). As eye-to-eye contact is one of the earliest social behaviors that infants engage in and is under the infant's own control, it is also interesting that sex differences have been found in this behavior. Hittelman and Dickes (1979) found that 24-60 hour old girls engaged in longer eye-to-eye contact with a female interactor than boys, although Leeb and Rejskind (2004) failed to replicate this finding in a sample of infants aged 13-112 hours. Nevertheless, the latter study showed that at age 3.5 months, girls engaged to a much higher extent than boys in mutual eye contact with an interactor, especially with the female interactor. Even though infant girls showed a large increase in mutual eye-contact with the interactors from the first to the second testing occasion, boys did not show an increase in amount of eye-contact with the interactors. Others have also shown that females in early and late infancy, childhood, and adulthood engage in mutual eye-contact to a higher extent than males, and particularly when the interactor is female (Ashear & Snortum, 1971; Exline, 1963; Exline, Gray, & Schuette, 1965; Field, Cohen, Garcia, & Greenberg, 1984; Levine & Sutton-Smith, 1973; Osofsky & O'Connell, 1977). In line with this, women have been found to attend more to the eyes than men when viewing faces, as shown by a higher number of fixations and a longer dwell time in the eye region (Hall, Hutton, & Morgan, 2010; Sæther, Van Belle, Laeng, Brennen, & Øvervoll, 2009).

It is not clear if there are early sex differences in face perception. For 2.5-4.9 year old children, Burns and Reynolds (1988) found that the magnitude of girls' advantage over boys in face identification was $d = 0.32$, and this difference remained when general intelligence was accounted for. However, results from a study by Picozzi, Macchi Cassia, Turati, and Vescovo (2009) indicated that 3- and 4-year-old girls and boys performed at a similar level, whereas 5-year-old girls seemed to perform at a higher level than 5-year-old boys in identification of female faces. Similarly, Ge and colleagues (2008) found that 4-, 8-, and 14-year-old girls were better at identifying their peers compared to boys when identification was based on facial features (i.e., nose, eyes, mouth), although girls' advantage over boys appeared to be larger for female than male faces.

For adults, there is some evidence of a sex differences in detection of faces, as women were more accurate and faster in identification of upright male face contours, slightly better than men and faster in the identification of inverted male face contours, and there was no sex difference in identification of tree contours (McBain, Norton, & Chen, 2009). Moreover, Godard and Fiori (2010) assessed sex differences in adults' identification of bisymmetric faces (a left and a right face half) and hemi-faces (left or right face half). The hemi-faces were presented either in the left or the right visual field. A target bisymmetric or hemi-face was presented shortly, and after a short ISI, a bisymmetric face either matching the face seen previously or a new face was presented and participants decided whether the face was the same as the one seen previously or not. They found that men were more accurate when the hemi-face was presented in the

left visual field, whereas women performed equally well for hemi-faces presented in either hemisphere. Even though there was no sex difference in accuracy, women responded faster than men (Godard & Fiori, 2010). In a more recent study, Godard and Fiori (2012) assessed discrimination of faces. Here, the probe face displayed different emotional expressions at the initial presentation, but a neutral expression during identification. There was no sex difference in performance when the probe displayed a neutral expression, that is, when the probe and the target were exactly the same. However, when the probe displayed an emotional expression, women were more accurate at identifying the neutral target than men were.

Megreya, Bindemann, and Havard (2011) investigated potential sex differences in matching of unfamiliar faces (same/different identity judgments). They found that women were more accurate when matching female faces, and performed better than men on mismatch trials. Finally, Cellerino, Borghetti, and Sartucci (2004) used Gaussian noise filters to assess the effect of reduced perceptual information on face gender categorization. They found that women identified female faces more accurately than men when picture quality was reduced, although it should be noted that male faces were generally more accurately classified as “male” than female faces were classified as “female”. Taken together, these findings indicate that women perform at a higher level and faster than men on face detection tasks, and on face discrimination tasks, which typically assess immediate identification of briefly displayed faces (e.g., 120 ms), following short ISIs (e.g., 1120 ms; Godard & Fiori, 2012).

1.3.2 Sex differences in face recognition

Sex differences in face recognition memory have been noted from age 6 and up (e.g., Cross, Cross, & Daly, 1971; Ellis, Shepherd, & Bruce, 1973; Feiman & Entwisle, 1976), and a recent large cross-sectional study of children, adolescents, and young adults (ages 8-21) showed a female advantage, which was not moderated by age (Gur et al., 2012). The sex difference in face recognition memory is also found in younger (Bengner et al., 2006; Chance & Goldstein, 1979; Herlitz & Yonker, 2002), middle-aged, and older adults (Herlitz et al., 1997). It is less clear if sex differences are present during infancy and early childhood. Even though few studies seem to have assessed sex differences in infants’ recognition of faces, there are some findings indicating that 5-6 month old girls were better than boys at discriminating between upright faces, but not inverted faces (Fagan, 1972, Experiment 3, 5). However, these findings were not replicated in a later study (Fagan, 1973), and another study found that 3-month-old boys, but not girls, recognized a female face, but there was no difference between 6-month-old girls and boys (Pascalis, de Haan, Nelson, & de Schonen, 1998).

There is some evidence of sex differences in BOLD responses during face processing, with men showing higher prefrontal activity than women (Fine, Semrud-Clikeman, & Zhu, 2009; Fischer, Sandblom, Nyberg, Herlitz, & Bäckman, 2007; Ino, Nakai, Azuma, Kimura, & Fukuyama, 2010; but see also Haut & Barch, 2006; Sergerie, Lepage, & Armony, 2006). It should be noted that most of these studies used neutral and emotional faces (Fine et al., 2009; Fischer et al., 2007; Ino et al., 2010). It has also been observed that men had a higher BOLD response in FFG or FFA than women (Ino et al., 2010; Mather, Lighthall, Nga, & Gorlick, 2010). On the other hand, girls and women

seem to show higher face specificity in FFG than boys and men, as evidenced by a larger volume of activated voxels in the fusiform region in response to faces (Golarai et al., 2010; Tahmasebi et al., 2012). Finally, studies assessing event-related potentials in response to faces have indicated that men show a more right-lateralized response over the occipito-temporal cortex than women, who show a bilateral response pattern (Proverbio, Brignone, Matarazzo, Del Zotto, & Zani, 2006; Proverbio, Riva, Martin, & Zani, 2010). This is in line with the behavioral findings discussed previously, indicating that men are better at processing faces presented to the left visual field than the right visual field (Godard & Fiori, 2010).

1.3.3 Women's advantage – an own-group bias?

Several studies show that face gender influences the magnitude of the sex difference in memory for faces. One of the first studies assessing the own-gender bias in children and adults' recognition memory for faces nicely illustrates the general performance pattern observed in more recent studies, as females recognized more female than male faces, whereas males did not display an own-gender bias (Sugisaki & Brown, 1916). Women's own-gender bias has been replicated in many studies (e.g., Lewin & Herlitz, 2002; Rehnman & Herlitz, 2007), whereas the pattern for men varies. A male own-gender bias has been noted in some studies (McKelvie, 1981; McKelvie, 1987, Experiment 3; Wright & Sladden, 2003), but others found that men recognized female faces better than male faces (Ino et al., 2010; McKelvie, 1987, Experiment 2; Rehnman & Herlitz, 2007), or no difference in men's memory for female and male faces (Going & Read, 1974; Lewin & Herlitz, 2002; Slone, Brigham, & Meissner, 2000; Sugisaki & Brown, 1916). In turn, girls' and women's advantage in face recognition memory is larger for female faces, whereas the female advantage in memory for male faces is typically smaller or non-existent (Bowles et al., 2009; Cross et al., 1971; Feinman & Entwisle, 1976; Lewin & Herlitz, 2002; O'Toole et al., 1998; Rehnman & Herlitz, 2006, 2007). Therefore, the two general patterns that earlier studies suggest are that women recognize more female faces than men and more female than male faces, and women have no (Pattern A) or a slight (Pattern B) advantage over men in recognition of male faces (see Figure 1).

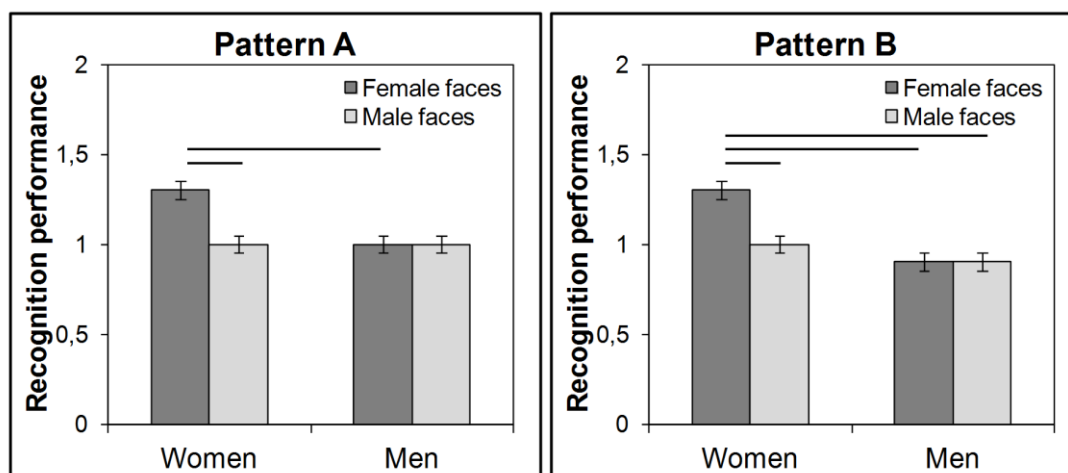


Figure 1. Hypothetical illustration of sex differences in memory for faces.

Many earlier studies have shown that members of one's own social and/or biological groups tend to be better remembered than other-group members. A well-replicated instance of this phenomenon is the own-race bias in memory for faces, showing that own-race faces are typically better remembered than other-race faces (for reviews and meta-analyses, see Anthony, Copper, & Mullen, 1992; Meissner & Brigham, 2001). Similarly, young adults often show an own-age bias, as young adult faces are better recognized than older adult faces or children's faces (for a meta-analysis, see Rhodes & Anastasi, 2012). If we view women's better memory for female than for male faces as an own-group bias in memory for faces, the sex difference in memory for female faces can be seen as a by-product of women's own-gender bias in memory for faces.

At which age does an own-gender bias in face processing and recognition appear? During infancy, both boys and girls seem to be better at processing female compared to male faces; infants require longer time during processing and recognition of male than female faces, they are better at matching a female voice with a female face than a male voice and face, and a female face prototype seems to emerge before a male face prototype (Ramsey, Langlois, & Marti, 2005). It has consistently been shown that girls from age 6 and older remember female faces better than male faces (Cross et al., 1971; Feinman & Entwisle, 1976; Rehnman & Herlitz, 2006), and this effect is found independent of face age and ethnicity (Cross et al., 1971; Rehnman & Herlitz, 2006). For boys, the pattern is less clear. Rehnman and Herlitz (2006) found that 9-year-old boys recognized own-race boys' faces better than girls' faces, whereas other studies have shown that boys recognized female and male faces with equal facility (e.g., Cross et al., 1971; Feinman & Entwisle, 1976). Even though Ge et al. (2008) assessed children's identification of peers and not recognition of unfamiliar individuals, their results are interesting with regard to the gender bias. They found that boys' identification of peers based on isolated internal features was similar for female and male facial features at ages 4 and 8, but 14-year-old boys identified more male than female peers given their internal features. Ge and colleagues (2008) suggested that, as a result of increasing preferences for same sex peers during childhood, differential experience with same- and other-sex peers co-occurs with general cognitive development, so that with increased age, children become more skilled at recognizing peers of the same sex, in turn being a precursor of the adult own-gender bias.

I will now review potential explanations of sex differences in memory for (female) faces and women's own-gender bias. Inherent in some of these explanations is whether we should consider these effects as separate or not, and in turn, do we need the same or different explanations for the two effects? I will return to these issues in the discussion.

1.3.4 Explanations of sex differences and the female own-gender bias

The following review is by no means exhaustive, and many of these explanations overlap. I have attempted to make predictions given the proposed explanations, as in some cases, none are provided by the authors.

Social explanations: Interest, sex-roles. The interest hypothesis has been suggested as a potential explanation for why girls remember more female faces than boys: "Girls [aged 12 and 17] are better than boys at recognizing female faces, which may reflect

their greater interest in female physiognomy, encouraged, perhaps, by the wealth of cosmetic advertising to which they are exposed” (Ellis et al., 1973, p. 174). Following this reasoning, McKelvie (1981) suggested that women’s advantage over men on female faces would only be present for familiar (e.g., same-race) and attractive faces, as women would not be expected to allocate more attention to female faces if they are less attractive than the male faces. Thus, for unfamiliar and/or unattractive faces, women should not remember more female faces than men as they would not use “their special inspection strategy” (McKelvie, 1981, p. 123). However, McKelvie (1981) also recognized that this might have been a suboptimal explanation, as it did not address why women also remembered more children’s faces than men did. Instead, he argued that interest in faces could be seen as a combination of exposure to faces and social conditioning, and that the interest hypothesis could be tested by using materials that men and women assumedly would be differentially interested in. As a later study showed a female advantage on adult female and children’s faces and a male advantage in memory for cars, this was taken as direct support for the interest hypothesis (McKelvie, Standing, St. Jean, & Law, 1993; see also Davies & Robertson, 1993). Given the interest hypothesis, then, women should not recognize more female faces than men if facial attractiveness is controlled for, and should not show an advantage on less attractive, unfamiliar, or out-group female faces (McKelvie, 1981). These predictions were tested in Study III, by assessing memory for own- and other-race faces and controlling for facial attractiveness.

The sex role hypothesis (Witryol & Kaess, 1957) suggests that the female sex role, which emphasizes social facility, influence and strengthen social skills primarily in women, which would lead women to remember both female and male faces better than men. One potential prediction of this hypothesis is that sex differences should be larger between men and women showing traditional sex role schemas (i.e., women with feminine and men with masculine gender schemas). Using the Bem sex role inventory, Rehnman and Herlitz (2007) assigned men and women into groups depending on whether they had feminine or masculine gender schemas and found no differences in face recognition memory performance depending on gender schemas, as participants with a more feminine gender schema did not perform at a higher level than participants with a more masculine gender schema.

1.3.4.1 Biological: Sex hormones and puberty

Puberty has been suggested as an important period with respect to the organization of female and male cognitive functions (e.g., Sisk & Zehr, 2005) and some have argued that sex hormones during puberty should be important for the organization of face processing and recognition (Scherf, Behrmann, & Dahl, 2012). Therefore, it could be speculated that sex differences in memory for faces may become larger during puberty, and/or that children with higher sex hormone levels and/or earlier pubertal maturation would show larger sex differences in memory for faces. This was assessed in Study I.

1.3.4.2 Cognitive and developmental theories

It has been suggested that women’s advantage over men could be a result of women verbalizing faces to a greater extent than men do, as women’s higher verbal ability may support their encoding of faces (Lewin et al., 2001). Now, faces are generally not easy

to verbalize, but if women would provide more descriptions of faces during encoding (e.g., “dark-haired, friendly-looking woman”), this may increase the probability of later recognizing these faces. Lewin and Herlitz (2002) showed that the sex difference in memory for faces remained when a composite consisting of verbal fluency and performance on a synonyms task was controlled for (see also Herlitz et al., 1997). Similarly, it has been suggested that women’s advantage for any material stems from their advantage on verbal episodic memory, and that if verbal episodic memory is controlled for, women’s advantage in memory for non-verbal materials should be attenuated, even though a small sex difference may still remain (Andreano & Cahill, 2009). Thus, if we control for performance on verbal episodic memory tasks, the sex difference in memory for female faces should be reduced. This was tested in an additional analysis of data from Study I.

Another suggestion is that women and men use different strategies while processing especially female faces, and that women’s encoding of female faces is more elaborate than men’s, which would lead to a more detailed encoding of faces, and in turn better memory. Divided attention at encoding has earlier been shown to reduce later recognition performance (e.g., Kellogg, 1980), and seem to change the encoding quality so that it becomes shallower and less elaborate (Naveh-Benjamin, Craik, Gavrilescu, & Anderson, 2000). Thus, divided attention at encoding may reduce women’s advantage in memory for (female) faces. This was tested in Study II.

The reason why women remember (female) faces better than men could also be a result of differential experience. Davies and Robertson (1993), as well as McKelvie et al. (1993), assessed sex differences in memory for faces and cars, and as females recognized more faces than males, and males more cars than females, the potential influence of sex differences in experience with each of the materials was discussed. From this perspective, women should not only remember more (female) faces than men, but also show an advantage on face processing tasks, and a greater degree of face specificity in the core face network. This is reasonable, as performance on perceptual face identification tasks is positively related to face recognition memory performance, but less so to recognition of other non-face objects such as houses (Wilhelm et al., 2010). Finally, and related to the expertise account, is the idea that women’s advantage for female faces compared to men stems from the expertise girls develop for females in infancy, which may be strengthened in childhood for girls, but not for boys as they may become more oriented towards other males (Ramsey et al., 2005; Ramsey-Rennels & Langlois, 2006).

1.3.4.3 Women’s own-gender bias

As women seem to mainly outperform men on female faces, and sex differences in memory for male faces are often small or non-existent, women’s advantage over men may be a result of their own-gender bias. As mentioned earlier, the interest hypothesis (McKelvie, 1981) may also be applicable to women’s own-gender bias. Others have proposed an evolutionary explanation, with female competition as the main factor (Maner et al., 2003), which would bias women in relationships with men to attend more to and recognize attractive female faces better than male faces – as these individuals are potential competitors threatening their relationships. However, perhaps of a larger

interest are frameworks that aim to explain own-group biases in general (Hugenberg, Young, Bernstein, & Sacco, 2010; Sporer, 2001).

There are two main perspectives on own-group biases, although they are also typically seen as complementary to each other (e.g., Sporer, 2001). The first holds that own-group biases result from differential experience. This perspective mainly focuses on the own-race bias in memory for faces, but has also been applied to the own-age bias (e.g., Macchi Cassia, 2011; Rhodes & Anastasi, 2012). According to this account, experience is greater for own-race compared to other-race faces, resulting in higher face processing skills and in turn better memory for own-race faces (for a review, see Meissner & Brigham, 2001). I will refer to this generally as the expertise hypothesis. The second is the socio-cognitive account, holding that interest, attention, and motivation create own-group biases in memory for faces (e.g., Hugenberg et al., 2010). When viewing an out-group face, a fast categorization response determines that this is an out-group face, which in turn leads to that this face is processed in a less efficient manner. This could mean less holistic processing, or that features associated with this out-group is focused on, which in turn leads to worse later recognition.

There is evidence supporting both accounts. In line with the expertise hypothesis, it has been shown that for Caucasians, the composite effect is larger for own-race faces (Michel, Rossion, Han, Chung, & Caldara, 2006), and own-race facial features are better identified when presented in a face but identification of other-race facial features is similar when presented in isolation or in a face (Tanaka, Kiefer, & Bukach, 2004). Moreover, changes to facial features and their spatial relation are detected more accurately in own-race compared to other-race faces (e.g., Rhodes, Hayward, & Winkler, 2006). These findings suggest that own-race faces are processed in a more holistic manner than other-race faces, but also that component coding of own-race faces may be better, which both may be a result of expertise for own-race faces (see also Hayward, Rhodes, & Schwaninger, 2008). In addition, self-reported experience with other-race individuals is related to a reduced own-race bias in memory (Chiroro & Valentine, 1995; Wright, Boyd, & Tredoux, 2003) and configural processing (Hancock & Rhodes, 2008; Rhodes et al., 2009). While this has not consistently been replicated (Ng & Lindsay, 1994; Slone et al., 2000), a meta-analysis indicated that there is a small but significant effect of other-race contact on the own-race bias in memory (Meissner & Brigham, 2001). Moreover, the gaze pattern during encoding of own-race faces differs from the one observed for other-race faces, as own-race faces receive a larger number of fixations, especially the eye region (Goldinger, He, & Papesh, 2009). However, it has been shown that mere exposure to other-race faces is not sufficient for expertise to develop for these faces (McGugin, Tanaka, Lebrecht, Tarr, & Gauthier, 2011; Tanaka & Pierce, 2009). In turn, the own-race bias could be a result of that people may be more likely to individuate own-race faces, and to process other-race faces at the category level (Levin, 2000; Tanaka & Pierce, 2009). Therefore, it has been proposed that individuation training, that is, practicing recognition of faces at a subordinate (individual) level, is more important for the development of expertise (e.g., McGugin et al., 2011).

In support of the socio-cognitive account, there are findings showing that the own-race bias can be reduced if participants receive information about the own-race bias and are

instructed to attend more to other-race faces before face encoding (Hugenberg, Miller, & Claypool, 2007), and own-group biases can be induced by labeling own-race faces as out-group and in-group members (Bernstein, Young, & Hugenberg, 2007). It has generally been suggested that own-race faces are more attended to during encoding (e.g., Meissner, Brigham, & Butz, 2005), and therefore better recognized than other-race faces. The relation between preferential viewing and memory for own- and other-race faces was assessed in Study III.

Similarly, some have proposed that own-race faces may be encoded more elaboratively than other-race faces, which would be a more attention demanding strategy (Meissner et al., 2005). If this is the case, manipulations that distract or interfere with attentional resources (such as a secondary task) during face encoding may reduce the own-race bias in memory for faces (e.g., Meissner et al., 2005). This may also be the case for women's own-gender bias. The effect of divided attention on the magnitude of women's own-gender bias was assessed in Study II.

As the FFG and IOG are preferentially engaged during face processing, and increased activity in these regions is potentially related to greater visual expertise, it is of interest to determine whether BOLD responses in these regions differ between own-race and other-race faces. Golby, Gabrieli, Chiao, and Eberhardt (2001) found that men's BOLD responses in FFA were higher for own- compared to other-race faces. Moreover, they correlated the difference in memory for own- compared to other-race faces with the BOLD response throughout the brain that was higher for own-race than other-race faces, and found that individuals with a higher BOLD response in left FFG also showed a larger own-race bias in memory for faces, and individuals with a higher BOLD response for other- than own-race faces had also better memory for other- compared to own-race faces. These findings have been replicated in a later study, using a categorization task and individually defined areas of FFG and IOG activation (Feng et al., 2011). Typically, when faces are categorized as being own- or other-race faces, responses are faster for other-race compared to own-race faces. Feng et al. (2011) found that faster categorization of other-race than own-race faces was associated with a larger difference in left FFA responses to own-race faces. Moreover, they also found that BOLD responses in OFA were higher for own- than for other-race faces. Taken together, there are a number of studies showing a higher BOLD response in FFG for own- compared to other-race faces (Feng et al., 2011; Golby et al., 2001; Kim et al., 2006). However, less is known about BOLD responses to female and male faces in core regions of the face network, and whether differential BOLD responses in left FFG is associated with the gender bias in memory for faces. This was tested in Study IV.

2 AIMS

The present thesis aimed to address potential mechanisms of sex differences in cognitive abilities, with a special focus on face recognition memory and the gender bias in memory for faces. The specific research questions were:

1. Are sex differences in cognitive abilities magnified during puberty, as a result of group differences in age, hormone levels, and/or pubertal development (Study I)?
2. Can the female advantage in verbal episodic memory explain sex differences in face recognition memory (see Andreano & Cahill, 2009)? That is, if verbal episodic memory performance is controlled for, do sex differences in memory for (female) faces remain (Study I)?
3. Can the female own-gender bias in face recognition be explained by women encoding female faces more elaborately than male faces? In Study II, divided attention at encoding was used to assess whether this manipulation would eliminate women's own-gender bias.
4. Does face gender influence men and women's attention and memory for own- and other-race faces (Study III)?
5. Do women, but not men, show a higher BOLD response in FFG and IOG to female compared to male faces during incidental face encoding? Is the difference in BOLD response of left FFG to female versus male faces related to the difference in memory for female and male faces? These questions were addressed in Study IV.
6. How consistent are sex differences in memory for faces and the own-gender bias in memory for faces across different studies and samples (Studies I-IV)?

3 METHODS AND RESULTS

3.1 STUDY I

The objective of this study was to assess whether sex differences in cognitive abilities were magnified during puberty, as a result of group differences in age, hormone levels, and/or pubertal development. If so, these findings would indicate that sex hormones have activational and/or organizational effects on the brain and in turn on girls' and boys' cognitive performance.

3.1.1 Participants

In this study, 102 girls and 85 boys aged 12-14 years participated. There was no sex difference in age (in months).

3.1.2 Materials and procedure

Participants completed the cognitive tasks in groups of six during the morning. The test battery comprised phonetic verbal fluency tasks (letters A, S), a verbal episodic memory task (free recall of 16 common nouns), a face recognition memory task (20 targets and 20 lures; see Lewin & Herlitz, 2002), and a mental rotation task (modified from Vandenberg, 1971). The order of the tasks was as follows: (1) presentation of faces (3 seconds [sec]/face); (2) presentation of words (3 sec/word); (3) free recall of words; (4) word recognition; (5) mental rotations (5 min); (5) face recognition memory (10 sec/face). Next, each participant met the test leader individually for collection of blood samples by venipuncture and to rate his or her puberty development using a booklet (girls, breast and pubic hair development; boys, genital and pubic hair development; Hall & Pilström, 1996, 1999). Also, each participant completed two verbal fluency tasks (A, S; 1 min/letter).

Serum levels of estradiol (E_2) were assessed using Auto DELFIA® Estradiol time-resolved fluoroimmunoassaykit (detection limit: 10.6 pmol/L); testosterone (T) with Auto DELFIA® testosterone-kit (detection limit: 0.02 nmol/L); sex hormone-binding globulin (SHBG) with Auto DELFIA® SHBGKit (detection limit: 0.5 nmol/L) (Wallac OY, Finland); p-albumin with Image™ Immunochemistry Systems (detection limit: 0.2 g/L) (Beckman Instrument AB).

3.1.3 Statistical analyses

As the serum level of total T does not capture the level of active testosterone (free T), levels of free T were computed using the Vermeulen formula, which assumes that the binding constants for albumin and SHBG are known (Vermeulen, Verdonck, & Kaufman, 1999).

To create groups of early and late maturers, the pubertal composite measure was regressed on age in months for boys and girls, separately. Individuals located above the regression line were categorized as early maturers, and individuals below the regression line were categorized as later maturers. Similarly, to assess the effect of low versus high sex hormone levels (boys, free T; girls, E_2), sex hormone levels were regressed on

age in months, and again, individuals located above the regression line were categorized as having high hormone levels, and individuals below as having lower hormone levels.

MANOVAs were used to assess the effects of (1) age (12, 13, 14), (2) pubertal maturation (early, late), and (3) sex hormone levels (high, low) on sex differences in cognitive performance on the various tasks. Pearson product-moment correlations were used to assess the relation between sex hormone levels and cognitive performance, and partial correlation analyses of these variables controlling for age in months.

3.1.4 Results

As expected, girls' and boys' levels of endogenous free T and E₂ differed, as boys had higher levels of free T than girls, and girls had higher levels of E₂ than boys. As expected, girls outperformed boys in verbal free recall, face recognition memory, and verbal fluency, whereas boys performed on a higher level than girls on mental rotations. Importantly, the analysis of age, pubertal maturation, and levels of sex hormones showed that (1) age did not interact with sex on any of the cognitive measures, (2) there were no differences on the cognitive tests between early or late maturers as assessed by self-rated puberty, and pubertal development (early, late) did not interact with sex of participant, (3) there were no differences on the cognitive tests between groups categorized as having high or low sex hormone levels, and there was no interaction between sex of participant and high versus low sex hormone levels. Finally, there were overall no relations between levels of sex hormones and cognitive performance for either boys or girls, apart from a weak positive association between E₂ and mental rotation performance for boys ($r = .23$). Correcting for multiple tests (Bonferroni), this relation was not significant ($p > .003$).

Conclusions. The results indicate that cognitive sex differences do not increase between ages 12-14, and that these differences are not magnified in early maturers, or in groups having higher levels of sex hormone. Further, little support was given for a relation between individual differences in sex hormone levels and cognitive performance.

3.1.5 Additional analyses and results

Note that the following analyses and results are not included in the manuscript. To assess the pattern of an own-gender bias in these age groups, as well as sex differences in memory for faces, hit and false alarm rates were computed for female and male faces, respectively. For each participant, 0.5 was added to his or her number of hits and false alarms, and each measure was divided by total number of trials plus one. Next, discrimination sensitivity, d' , was computed (e.g., Snodgrass & Corwin, 1988) for female and male faces. A mixed ANOVA was computed, assessing the effects of sex, age in years, and face gender on d' .

Next, to assess whether the sex difference in memory for female faces was reduced when individual differences in verbal episodic memory were held constant, a latent measure of verbal episodic memory was created from performance on two verbal episodic memory tasks, free recall and word recognition (hits – false alarms). These

variables were not normally distributed and were therefore transformed. The word recognition variable was reflected; the square root was taken and the variable was reflected again. The transformation resulted in an acceptable level of skewness (-1.60). For free recall, no transformation resulted in an acceptable level of kurtosis. Therefore, this variable was visually binned into seven categories (kurtosis = -0.17). Next, the two variables were transformed into Z-scores. The relation between word recognition and recall was of moderate size, $r(185) = .59, p < .001$. The variables were entered into a principal component analysis using direct oblimin rotation. The one factor solution explained 79.68% of the variance in free recall and word recognition memory. The scores from this solution were saved (method = regression) and used as a control variable in the analysis of sex differences in memory for female faces. To assess whether the expected advantage for girls in memory for female faces remained after controlling for verbal episodic memory, a linear regression analysis was run. Recognition performance (d') for female faces was used as the dependent variable. Sex of participant and age in months were added as predictors in a first step, followed by the latent verbal episodic memory variable. All predictors were mean centered.

The mixed ANOVA showed that girls recognized more faces than boys, $F(1, 181) = 9.22, p = .003, \eta_p^2 = .05$. In addition, female faces were recognized better than male faces, $F(1, 181) = 7.83, p = .006, \eta_p^2 = .04$. As expected, there was an interaction between face gender and sex of participant, $F(1, 181) = 29.54, p < .001, \eta_p^2 = .14$, showing that girls recognized more female faces than boys did, $t(185) = 4.93, p < .001, d = 0.72$, and that there was no sex difference in memory for male faces, $t(185) = -0.75, p = .46$. Girls recognized more female than male faces, $t(185) = 5.78, p < .001, d = 0.67$, whereas there was a trend for boys to recognize male faces better than female faces, $t(84) = -1.84, p = .07, d = -0.21$. Finally, there was an effect of age, $F(2, 181) = 4.50, p = .01, \eta_p^2 = .05$. Post-hoc tests (LSD) showed that the 12-year-olds recognized faces less well than the older age groups ($ps < .03$), while there was no significant difference between ages 13 and 14 in memory for faces ($p = .53$). The interaction between sex and age of participant was not significant, $p = .47$. Similarly, there was no interaction between face gender and age of participant, $p = .42$. Finally, even though the three-way interaction was not significant, $p = .07$, the presence of gender biases for boys and girls was assessed separately in each age group. An own-gender bias was present for girls in all age groups: age 12, $t(37) = 1.99, p = .05, d = 0.38$; age 13, $t(25) = 3.93, p = .001, d = 0.90$; age 14, $t(37) = 4.27, p < .001, d = 0.84$. In contrast, boys aged 12 and 13 years did not show a gender bias, but 14-year-old boys did: age 12, $t(21) = -.56, p = .58, d = -0.12$; age 13, $t(34) = -0.30, p = .77, d = -0.05$; age 14, $t(27) = -2.26, p = .03, d = -0.48$ (see Figure 2).

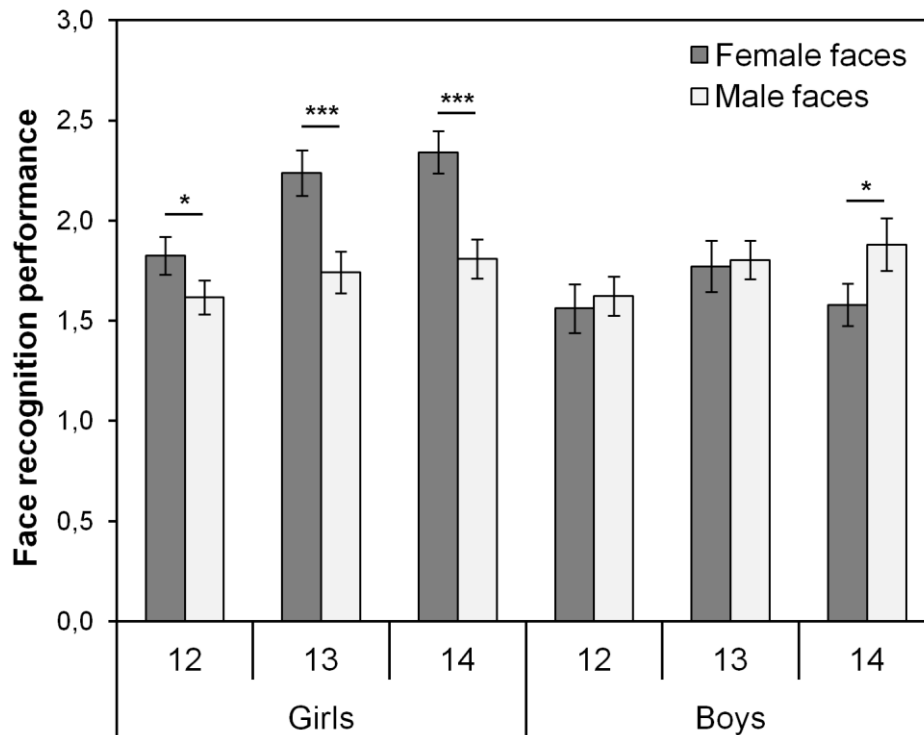


Figure 2. Girls' and boys' average memory performance (d') for female and male faces by age. Error bars represent standard error of the mean.

*** $p \leq .001$; * $p \leq .05$.

Finally, the linear regression analysis showed that girls' advantage in recognition memory for female faces remained after controlling for the latent verbal episodic memory factor (see Table 1). There was no significant interaction between sex and verbal episodic memory ($p = .10$), showing that the relation between verbal episodic memory and face recognition performance was similar in boys and girls. No other interactions between the predictors were significant ($ps > .08$).

Table 1. Effects (β -values) of sex and age on recognition memory (d') for female faces, before and after controlling for verbal episodic memory.

Predictors	Step 1	Step 2
Sex	.34***	.31***
Age (in months)	.19**	.17*
Verbal episodic memory		.17*
R^2	.14	.17

Note. *** $p < .001$, * $p < .05$.

Conclusions: As expected, girls aged 12-14 years showed an own-gender bias, and recognized more female faces than boys. In contrast, only 14-year-old boys showed an own-gender bias, whereas 12- and 13-year-old boys recognized female and male faces with equal facility (see also Ge et al., 2008). Finally, higher verbal episodic memory was related to better face recognition performance, but the sex difference remained,

suggesting that girls' advantage in memory for faces cannot be attributed to their advantage in verbal episodic memory.

3.2 STUDY II

The main objective of this study was to assess whether women's own-gender bias was attenuated by divided attention at encoding. This was of interest, as divided attention at encoding seems to prevent elaborate encoding strategies; if women's own-gender bias was a result of women encoding female faces more elaborately than male faces, this effect should be reduced. In addition, we assessed whether women's advantage over men in memory for female faces under full attention conditions remained when attention was divided at encoding.

3.2.1 Participants

In Experiment 1, there were 35 women and 32 men in the full attention condition, and 35 women and 32 men in the divided attention condition. Participants were between 17 and 43 years old ($M = 24.66$, $SD = 4.57$). In Experiment 2, 28 women and 16 men participated, aged 19-43 years ($M = 24.76$, $SD = 6.09$). Experiment 3 included 54 women and 25 men, aged 17-24 years ($M = 18.09$, $SD = 1.19$). There were no sex differences in age, years of higher education, or in vocabulary performance. The expected sex difference in mental rotation performance was found for participants in Experiments 1 and 2, but not for participants in Experiment 3.

3.2.2 Materials and procedure

In each experiment, there were two face recognition tasks. Twenty faces (10 female, 10 male) were presented (3 sec/face) during encoding. These target faces and an equal amount of distractors were presented during the yes/no recognition test (5 sec/face). To divide attention during face encoding, participants performed an auditory task while learning faces. In the first experiment, participants monitored a prerecorded list of digits presented with a rate of one digit per second, and the task was to detect whenever two odd digits were presented, and report the digits in the correct order aloud. In experiment 2, the same task was used, but participants instead wrote down the detected target digit sequences on a sheet of paper. In the secondary task of experiment 3, digits were presented at a rate of one digit per 2 seconds.

Each participant was tested individually in Experiment 1 and in groups in Experiment 2 and 3. In all three experiments, participants completed two face recognition tasks, one with divided attention at encoding, and one with full attention at encoding. In the first experiment, a between-groups design was employed for the analysis of attention at encoding, as one recognition memory test was excluded because of issues with a highly distinct male face in that set. In the second and third experiments, two new sets of faces were used that both had been matched for distinctiveness of female and male faces.

3.2.3 Results

Results showed that women recognized more female than male faces, independent of whether faces had been encoded with full or divided attention. Thus, even though face recognition memory was markedly reduced by divided attention, the magnitude of

women's own-gender bias in memory for faces remained. Given that the divided attention task used in the first two experiments was demanding, and in turn, recognition performance was very low, we also assessed whether women's own-gender bias remained if the divided attention task was made easier. Again, the effect was replicated. Finally, we noted that in each experiment, women only recognized more female faces than men in full attention conditions, suggesting that full attention at encoding may be required for women to excel over men in memory for female faces.

Conclusions: Divided attention at encoding did not reduce the magnitude of women's own-gender bias, even though later face recognition memory was impaired by divided attention. In turn, women's own-gender bias does not seem to be a result of effortful processing. In contrast, women's advantage on female faces over men was reduced by divided attention, showing that the manipulation had a differential effect on women's own-gender bias and the sex difference in memory for female faces.

3.3 STUDY III

Previous research suggests that the own-race bias in memory for faces is a result of other-race faces receiving less visual attention at encoding. As women typically display an own-gender bias in memory for own- and other-race faces (Cross et al., 1971; Rehnman & Herlitz, 2007; Slone et al., 2000) and men do not, we investigated whether face gender and sex of viewer influenced visual attention and recognition memory for own- and other-race faces, and if preferential viewing of own-race faces contributed to the own-race bias in memory.

Further, it has been suggested that women show an own-gender bias for familiar and attractive faces, and that they recognize more female faces than men when the female faces are familiar and attractive (McKelvie, 1981). Although not a main aim of the study, I will also report here whether the presence of women's own-gender bias and advantage over men remained when facial attractiveness was controlled for, and whether familiarity (race of face) influenced the effects.

3.3.1 Participants

The final sample consisted of 52 Swedish participants (28 women) between ages 17-37 ($M = 22.98$, $SD = 4.63$). There were no sex differences in age, years of higher education, or in vocabulary performance.

3.3.2 Materials and procedure

The viewing task consisted of 40 faces, with an equal number of Swedish, Bangladeshi, female, and male faces. Pairs consisting of an own-race and an other-race face were presented for 8 sec each. The gender of the face pairs was always the same. The order, combination, and position of the screen (left, right) were randomized across participants. The face recognition task included all previously seen faces, and an equal number of distractor faces from each face category. During the surprise recognition test, faces were presented at a rate of 5 sec per face, and participants indicated yes/no recognition with a button press.

All participants were tested individually. Before completing the tasks, they had been informed that the aim of the study was to assess how people look at different pictures, and that their gaze would be recorded by an eye-tracker. Participants viewed pictures of faces and landscapes before the presentation of own- and other-race faces, and after this, another set of faces. After approximately ten minutes, they completed the surprise recognition memory test.

Ten women and ten men not participating in the main study rated facial attractiveness and distinctiveness. Participants' scores for each face were averaged and included in additional control analyses of viewing time and memory for faces.

3.3.3 Statistical analyses

For the eye-tracking data, the face initially gazed upon was determined, as well as the total looking time for each face. Total viewing time was aggregated within each person for the mixed ANOVA analysis that was run to assess potential differences in viewing time depending on sex of viewer, face gender and race.

For the analysis of initial gaze to own- and other-race faces, random-intercept logistic regression analyses were run. All trials in which the participant's gaze was not at the fixation cross were excluded. The analysis was run for female and male faces separately. The dependent measure was the side of the screen that the participant had first gazed upon (left, right), and predictors were the side of the screen on which an other-race face had appeared.

Faces were also rated for distinctiveness and attractiveness by a group of men and women not participating in the main experiment. These scores were used to create averaged values of distinctiveness and attractiveness for each face, in order to control for these variables in the analyses of total viewing time and recognition memory. Random-intercept regression models were run to control for potential effects of attractiveness and distinctiveness on viewing time and memory for faces.

Finally, to test whether the own-race bias in memory for faces was reduced when viewing time was controlled for, a random-intercept logistic regression analysis was run, with later recognition of each face as the outcome, predicted by gender and race of face in a first step, and then controlling for viewing time in a second step.

3.3.4 Results

The findings from Study III showed that (1) other-race male faces received the initial gaze more often than own-race male faces, but there was no difference between initial gaze to own- and other-race female faces; (2) own-race females were overall viewed longer than other-race females, whereas the difference was smaller for own- and other-race male faces; (3) women recognized more female than male faces, independent of face ethnicity, whereas men overall recognized female and male faces to an equal extent. Moreover, the own-race bias was larger for female than for male faces. (4) Controlling for viewing time did not reduce the own-race bias in memory for (female) faces.

Controlling for attractiveness and distinctiveness did overall not influence these results, with the exception for total viewing time, as the difference between own- and other-race male faces was significant when attractiveness was held constant. Thus, own-race faces were viewed longer than other-race faces, although the difference was larger for female faces.

Conclusions: Women recognized more female than male faces and more female faces than men, independently of ethnicity of the viewed faces. Men recognized men and women equally well. Moreover, women's own-gender bias and advantage over men in memory for female faces remained when facial attractiveness was controlled for, suggesting that differential interest or attention in especially attractive (own-race) female faces cannot explain these effects. Finally, longer viewing time of own-race female compared to other-race female faces could not explain the difference in memory for these faces.

3.4 STUDY IV

The aim of study IV was two-fold: (1) to assess whether women showed higher BOLD responses in FFG and IOG to female compared to male faces; and (2), if there was a relation between differential BOLD responses in left FFG and the difference in memory for female and male faces. These questions were addressed in an event-related fMRI study using an individual ROI-based approach. This would address whether women's own-gender bias in memory for faces resembles findings for the own-race bias, showing higher BOLD responses in core face processing regions for own- than for other-race faces (e.g., Feng et al., 2011). In addition, we investigated whether there were sex differences in brain activity in these regions during face encoding.

3.4.1 Participants

The final sample included 15 women and 14 men between ages 20-31 ($M = 25.13$, $SD = 3.38$). There were no sex differences in years of education or in vocabulary performance.

3.4.2 Materials and procedure

Twelve young female faces, 12 young male faces plus 24 older adult faces were selected for the incidental encoding session. During this session, faces and a low-level perceptual baseline stimulus were presented for 3.5 sec each, followed by a random jitter during which a fixation cross was presented ($M = 3.5$ sec). Participants were instructed that they were to see faces, and to watch these as if they were at home watching TV while they were being scanned. After approximately 10 minutes, participants completed a surprise face recognition task in the scanner (also including 12 young female lures, 12 young male lures, 24 older adult lures). The focus of Study IV was on incidental encoding of own-age faces. Therefore only fMRI data from the encoding session and behavioral data from the recognition session were included in the analyses.

3.4.3 Statistical analyses

The 206 volumes acquired during the incidental encoding session for each participant were preprocessed using standard protocols (slice time corrected, realigned, and normalized). For each individual, a general linear model was run, including the onset times for each face category, the baseline stimulus, as well as 6 movement parameters and an intercept as regressors.

ROIs were specified on an individual basis, as activity in FFG and IOG to faces (> baseline) in clusters of 8 or more voxels significant at the threshold $p < .0001$ (uncorrected). The threshold had to be relaxed for four participants in order to define functional ROIs in IOG ($n = 3$, $p < .001$, uncorrected; $n = 1$, $p < .05$, uncorrected). For each individual, the average parameter estimates for female and male faces were extracted, in left and right FFG and IOG, respectively.

For the correlational analyses, difference scores were computed (parameter estimate female faces – parameter estimate male faces) in each hemisphere and region separately, for each individual. Similarly, difference scores were created from each individual's memory for female versus male faces ($d'_{\text{female faces}} - d'_{\text{male faces}}$).

3.4.4 Results

Women recognized more female faces than male faces, and that there was overall no difference in men's memory for female and male faces. Importantly, we found that women indeed showed a higher BOLD response in FFG and IOG to female than to male faces, whereas the differences were not reliable for men. Across men and women, a higher BOLD response in left FFG to one gender compared to the other was associated with better memory for that gender. In addition, we also found that men had a higher BOLD response than women to male faces in left FFG and right IOG (see also Ino et al., 2010; Mather et al., 2010).

Conclusions: Women showed a higher BOLD response in FFG and IOG to female than male faces, recognized more female than male faces, whereas there were no differences in men's recognition and BOLD responses to female and male faces. Across men and women, the difference in left FFG BOLD response to female and male faces was related to the difference in memory for female versus male faces. These findings suggest that differential BOLD responses in left FFG may underlie the bias to recognize one gender better than the other.

3.5 MINI-META-ANALYSIS: STUDIES I-IV

For descriptive purposes, weighted average effect sizes were computed from the results of Studies I-IV (see Table 2, Total [I-IV]), and represent the average effect sizes for full attention conditions and own-race faces. Effect sizes were combined using a fixed effects model (for formulas, see Borenstein, 2009; Shadish & Haddock, 2009).

Table 2. Effect sizes for the gender bias and sex differences in memory for female and male faces in Studies I-IV. A positive effect size for the gender bias indicates that more female than male faces were recognized, whereas a negative value indicates that more male than female faces were recognized. A positive value of the sex difference indicates a female advantage; a negative value indicates a male advantage. Weighted average effect sizes are found in the row Total (I-IV).

	<i>n</i>		Gender bias		Sex difference	
	Girls/ Women	Boys/ Men	Girls/ Women	Boys/ Men	Female faces	Male faces
Study I						
Age 12	38	22	0.38	-0.12	0.46	-0.02
Age 13	26	35	0.90	-0.05	0.70	-0.11
Age 14	38	28	0.84	-0.48	1.26	-0.11
Total (Study I)	102	85	0.67	-0.21	0.72	-0.11
Study II						
Experiment 1	35	32	0.75	0.07	1.06	0.29
Experiment 2	28	16	0.42	-0.31	0.65	-0.03
Experiment 3	54	25	0.66	0.07	0.49	-0.11
Total (Study II)	117	73	0.61	-0.03	0.78	0.15
Study III						
Own-race faces			1.11	0.71	0.45	-0.03
Other-race faces			0.59	-0.01	0.47	-0.10
Total (Study III)	28	24	1.26	0.33	0.72	-0.15
Study IV	15	14	0.65	0.03	0.59	-0.09
Total (I-IV)	262	196	0.67	-0.05	0.71	0.01

Note. For Study II, effect sizes from the full attention conditions are presented. All effect sizes were computed from measures of d' . The total effect sizes presented separately for each study were computed across all participants in the given study (i.e., effect sizes were not weighted by subsamples).

Conclusion: Results are consistent with previous findings, showing that the female own-gender bias is substantial and replicable across studies using different samples and procedures. Men, on the other hand, do not show a gender bias. Further, women consistently outperform men on female faces, but there is no sex difference in memory for male faces.

4 DISCUSSION

In this thesis, my aims were to target potential explanations of sex differences in cognitive abilities (i.e., mental rotation, verbal fluency, verbal episodic memory, face recognition), with a special focus on the mechanisms and explanations of the sex difference in memory for female faces and the female own-gender bias in memory for faces. I will now turn to discuss the specific research questions.

4.1 THE ROLE OF PUBERTY AND SEX HORMONES

Results of Study I replicated the commonly observed pattern of sex differences, with a male advantage in mental rotations (e.g., Voyer et al., 1995), and a female advantage in verbal fluency and episodic memory for faces and words (e.g., Kramer et al., 2001). However, these results did not support the idea that sex differences in cognitive abilities are magnified during puberty. This is very much in line with previous cross-sectional studies of cognitive sex differences across childhood and adolescence, showing that sex differences were not magnified between ages 10-14 (e.g., Gur et al., 2012). In addition, the magnitude of sex differences did not differ between groups of individuals with earlier or later pubertal maturation, or individuals with higher or lower levels of sex hormones. These findings suggest that earlier pubertal maturation or higher levels of sex hormones do not magnify cognitive sex differences, as would be expected if the changes during puberty would affect cognitive abilities in a sex-typical manner (i.e., enhancing performance on tasks that show sex differences in adults). Moreover, Study I failed to show consistent relations between individual differences in sex hormone levels and cognitive performance on the tasks. Two earlier studies indicated that higher levels of T were related better spatial performance in young and older adolescent boys (Davison & Susman, 2001; Hassler, 1992), but no relation between boys' mental rotation performance and levels of free T was found in Study I. There are few studies on children in this age span, but as for now, results are largely inconsistent and no relations between individual differences in sex hormone levels and cognitive performance have successfully been replicated.

Conclusion: Sex differences in cognitive abilities are not magnified during early adolescence, and are not larger for earlier maturers, or children with higher levels of sex hormones. These findings suggest that sex differences in spatial (and other) abilities are not a result of pubertal maturation or its associated changes in girls' and boys' levels of sex hormones, which seems reasonable as these sex differences are found much earlier than the typical ages in which pubertal development begins. Therefore, the reasons for sex differences in cognitive abilities should be sought after earlier in development. Finally, there were no consistent relations between girls' and boys' levels of sex hormones and performance on the various cognitive tasks. This adds to the wealth of mixed findings in this area, suggesting that there are no relations between individual differences in sex hormone levels and performance on verbal fluency, mental rotations, or episodic memory for faces and words (e.g., Davison & Susman, 2001; Hassler et al., 1992; Janowsky et al., 1998; Moffat & Hampson, 1996).

4.2 VERBAL EPISODIC MEMORY AND SEX DIFFERENCES IN MEMORY FOR FACES

The additional analyses of data from Study I showed that girls' advantage in memory for female faces remained when verbal episodic memory was controlled for. Even though there was a relation between verbal episodic memory performance and memory for female faces, and girls performed at a higher level than boys on these two measures, it is clear that the sex differences in these two abilities to a large extent are independent. This is in line with evidence from lesion studies (Farah et al., 2000; Moscovitch et al., 1997) and correlational findings of studies using structural equation modeling (e.g., Wilhelm et al., 2010), suggesting that face processing is a specific ability, in the sense that good face recognition performance does not necessarily imply that you perform well on recognition tasks of non-face materials. This finding, and others', showing that women's advantage in memory for faces is not reduced by controlling for verbal abilities (Herlitz et al., 1997; Lewin & Herlitz, 2002), clearly illustrates the notion that the sex difference in memory for female faces is independent from the sex differences in verbal fluency and verbal episodic memory.

Conclusions: Most findings suggest that the sex differences in episodic memory are highly dependent on the material, favoring females on words and faces, and favoring males on visuospatial materials, all tapping their own specialized ability and related brain networks. Even though women's advantage over men in verbal episodic memory and memory for odors may be linked to women's ability to verbalize the material (Larsson et al., 2003), this is not the case for the female advantage in memory for female faces.

4.3 THE ROLE OF ATTENTION

In Study II, we asked the question whether women use more elaborate strategies when encoding female compared to male faces, resulting in the female own-gender bias in memory for faces. To test this hypothesis, a divided attention task was used at encoding of faces to reduce any type of elaborate encoding or encoding strategies. The three experiments of Study II showed that women's own-gender bias remained when attention was divided at encoding. This suggests that women may encode female faces more efficiently than male faces when available attentional resources are greatly reduced and possibly, that women's own-gender bias stems from more efficient perceptual processing of female faces during encoding (Megreya et al., 2011).

Even though full attention is not necessary for later recognition, it is important for optimal recognition performance (e.g., Kellogg, 1980). It is not fully clear which aspects of encoding that divided attention affects, but it has been suggested that divided attention may affect several types of processing, such as initial registration of the material, and later elaborate processing (for a discussion, see Naveh-Benjamin, Guez, & Marom, 2003). Moreover, divided attention at encoding of words attenuates prefrontal and medial temporal lobe brain activity in regions related to encoding (Anderson et al., 2000; Iidaka, Anderson, Kapur, Cabeza, & Craik, 2000), and has been shown to reduce brain activity in material-specific regions. For instance, regions in the temporal lobe associated with reading and writing showed less activity with divided

attention during encoding of word pairs (Anderson et al., 2000). Thus, even when the quality of the encoding may have been greatly reduced by divided attention, women still recognized female faces to a higher extent than male faces.

In contrast to women's own-gender bias, there were no sex differences in the recognition of female faces when attention was divided at encoding. Even in the third experiment, in which an easier secondary task was used, women did not recognize more female faces than men did. Why? One suggestion is that if divided attention at encoding reduced the BOLD response in material-specific regions, such as FFG, this may lead to a disproportional impairment of women's performance on female faces compared to men's, as women seem to have overall a lower BOLD response in FFG to faces than men. This has also been noted for activity in the prefrontal cortex, with men showing a higher BOLD response to faces during encoding (e.g., Ino et al., 2010). This could also be an indicator as to why women's advantage for female compared to male faces remained when attention was divided – female faces could still evoke higher activity in FFG than male faces, as a general attenuation of brain activity may be expected.

Conclusion: Women do not appear to put more effort into encoding female than male faces, instead, women's encoding of female faces seems to be more efficient than for male faces, which may be related to perceptual expertise for female faces.

On the other hand, women may require full attention to outperform men in recognition of female faces, suggesting that women's memory for female faces relative to men is more sensitive to the effects of divided attention.

4.4 THE INFLUENCE OF FACE GENDER ON THE OWN-RACE BIAS

In Study III, we found that face gender modulated the own-race bias in attention and memory for faces. Other-race male faces received the initial gaze to a somewhat higher extent than own-race male faces. This bias may be linked to the potential threat that may be associated with out-group male faces (Navarrete et al., 2009). However, over time, own-race faces were viewed longer than other-race faces, with a larger difference in viewing time for female than male faces. In addition, the own-race bias was magnified for female faces, whereas it was not statistically reliable for male faces. It may be the case that the design of Study III reduced the own-race bias for male faces, as there are findings showing that the presence of an other-race male may reduce later recognition of own-race males (Kleider & Goldinger, 2001). On the other hand, Rehnman and Herlitz (2007) also found a magnified own-race bias for female faces, when faces were presented one at a time during encoding.

As differential attention at encoding has been suggested as a crucial factor strengthening the own-race memory bias, we assessed whether controlling for viewing time would decrease it. This was of particular interest as own-race female faces were better recognized than other-race female faces, and also viewed longer than other-race female faces. Even though longer viewing time at encoding was related to a higher probability of recognizing a face, controlling for viewing time did not change the magnitude of the own-race bias for (female) faces. Thus, merely viewing an own-race

face longer than an other-race face does not necessarily mean that this difference induces an own-race bias.

Moreover, Study III shows the importance of linking viewing time to face recognition at the item level. An earlier study computed difference scores for viewing time during encoding of own- and other-race faces, and for recognition memory of own- and other-race faces, and then correlated the two (e.g., He, Ebner, & Johnson, 2011). Using this procedure, I created difference scores for the own-race bias in total viewing time and in memory for faces. There was a positive correlation between the difference scores ($r[50] = .30$), which some would interpret to show that longer viewing of own-race faces can explain or contribute to the own-race bias in memory. In contrast, results of the random intercept analysis in Study III showed there was a relation between viewing time and later recognition, although the own-race bias in memory remained when viewing time was controlled for. Thus, analyzing the data on the item level or the aggregated level answers different questions – can viewing time explain the difference in later recognition – or, do individuals showing a larger bias in viewing for own- compared to other-race faces have a larger own-race bias in memory? It is clear that even though there may be a tendency for individuals showing a larger own-race bias in memory to view own-race faces longer than other-race faces, and faces viewed longer having a higher probability of being recognized later, it is not necessarily so that longer viewing time of own-race faces leads to that these faces are better recognized. If so, viewing time would have accounted for a larger part of the variance in recognition of own- and other-race faces.

Finally, we found that women showed an own-gender bias for both own- and other-race faces (see also Rehnman & Herlitz, 2007), and that their better recognition of female compared to male faces remained when facial attractiveness was controlled for, which is not in line with the interest hypothesis (e.g., McKelvie, 1981). It is interesting that young adult women's own-gender bias generalizes to less familiar faces, as it has also been noted for faces of children (Rehnman & Herlitz, 2007) and older adults (Mason, 1986).

Conclusion: Face gender may modulate the own-race bias, as the own-race effects are more pronounced for female than male faces. Own-race female faces seem to be special compared to other-race female faces, in the sense that both men and women preferentially attend to them and recognize them better. On the other hand, other-race male faces seem to attract the initial attention more often than own-race faces, suggesting that it may be of a higher functional importance to attend to these individuals. Viewing time cannot fully account for the higher probability of recognizing an own-race compared to an other-race face.

4.5 THE INFLUENCE OF FACE GENDER ON BRAIN ACTIVITY

Study IV showed that women's BOLD response in FFG and IOG was higher for female than for male faces. Moreover, the results showed that a relatively higher BOLD response in left FFG to one gender compared to the other was related to better memory for that gender. These results are very much in line with findings on the own-race bias (e.g., Feng et al., 2011; Golby et al., 2001), suggesting that the same pattern holds for

women, being the group commonly showing an own-gender bias in memory for faces. Interestingly, men did not show differential BOLD responses to female and male faces, and they recognized female and male faces with equal facility.

A higher BOLD response in FFG and IOG for own- compared to other-group faces has previously been interpreted to either suggest expertise with own-group faces, or that these faces are more attended to (e.g., Feng et al., 2011; Golby et al., 2001). It is difficult to discern what differential FFG responses represent, as BOLD responses in FFG (FFA) may be modulated by attentional demands (Wojciulik, Kanwisher, & Driver, 1998) as well as by expertise with the material (e.g., Bilalić et al., 2011).

It is interesting to note that differences in the magnitude of left FFG responses to female and male faces were related to the gender bias in memory. A higher BOLD response in FFG during encoding has also been shown for later recognized compared to forgotten faces (Prince, Dennis, & Cabeza, 2009), suggesting that the FFG supports successful facial encoding processes. For the findings of Study IV, this suggests that the category of faces recognized better engaged the (left) FFG to a higher extent during encoding than faces that were not recognized as well. It should also be noted that participants in Study IV did not know that a face recognition test would follow, suggesting that such encoding processes would not have been strategic.

Of interest is that we observed a sex difference in left FFG and right IOG, with men showing a higher BOLD response than women to male faces (see also Ino et al., 2010; Mather et al., 2010), in the absence of a sex difference in memory performance. As in Study IV, Ino et al. (2010) did not observe sex differences in memory for faces, but found that men generally activated more brain areas than women during encoding of faces. Some of these areas were bilateral FFG and right IOG; but of these regions, men only showed a higher response than women to male faces in the right FFG. Ino et al. (2010) suggested that women processed faces more efficiently than men, and therefore required a lower BOLD response while performing at a similar level as men did. In line with the idea that women may show markers of more efficient face processing at the neural level than men, Golarai et al. (2010) found that adolescent girls and women showed more face-specific BOLD responses than adolescent boys and men did, as evidenced by a larger number of activated voxels in FFG to male faces compared to common objects (see also Tahmasebi et al., 2012). In contrast to the whole brain approach used by Ino et al. (2010), Golarai et al. (2010) used a localizer task and individually defined ROIs.

Conclusion: Women show higher BOLD response to female than male faces in core regions of the face network during incidental encoding, while also recognizing more female than male faces. Men do not differentiate between female and male faces, neither in memory performance nor in BOLD responses. In turn, these findings may indicate that women are experts on female compared to male faces.

4.6 MINI-META-ANALYSIS: STUDIES I-IV

Results from Study I showed that girls' advantage over boys in memory for female faces were present for all age groups. This is what one would expect, given the studies

showing that girls from about the age of 6 and onwards recognize more female faces than boys, and more female than male faces (Cross et al., 1971; Ellis et al., 1973; Feinman & Entwisle, 1976).

As expected, girls' own-gender bias was present at ages 12-14 (e.g., Cross et al., 1971). An own-gender bias was also observed for 14-year-old boys (cf., Ge et al., 2008), but it is not clear whether this is a chance finding, or if boys indeed at this age show an own-gender bias. Twelve- and 13-year-old boys recognized female and male faces with similar facility, and other studies have not consistently reported an advantage for boys on male compared to female faces (Cross et al., 1971; Ellis et al., 1973; Feinman & Entwisle, 1976; Rehnman & Herlitz, 2006).

Finally, the mini-meta-analysis of Studies I-IV of the present thesis showed that the female own-gender bias and the female advantage over men in memory for female faces were consistent and of medium size. For men, it is clear that they do not show an own-gender bias at the group level, and across the four studies, there was no sex difference in memory for male faces.

4.7 MECHANISMS OF WOMEN'S OWN-GENDER BIAS AND SEX DIFFERENCES IN MEMORY FOR FACES

Generally, the results of the present thesis confirm previous observations: women show an own-gender bias, whereas men do not, and women excel over men in memory for female faces but not for male faces (e.g., Lewin & Herlitz, 2002; McKelvie, 1987). Does this mean that the sex difference in memory for female faces is a result of women showing an own-gender bias in memory for faces, whereas men do not?

4.7.1 Is women's advantage over men specific for female faces?

There are findings suggesting that women have an advantage over men also in processing of and memory for male faces. McBain et al. (2009) assessed potential sex differences in detection of male facial contours, tree contours, and on male facial identity discrimination. In the detection task, women's advantage was largest for upright faces, smaller for upside-down faces, and there was no difference between men and women in identification of tree contours. Women did not outperform men in the easiest condition of the identity discrimination task, which had a short ISI (0.5 sec) between encoding and test. However, women performed at a higher level than men in the two more difficult conditions, one with a longer ISI (3 sec), and one with visual noise added to the images (cf. mismatch trials, Megreya et al., 2011).

Similarly, Bowles et al. (2009) found that women had an advantage over men on both the Cambridge Face Memory Test (CMFT) and the Cambridge Face Perception Test (CFPT), two tasks that only include male faces. In turn, they argued that women's advantage over men could not be interpreted as an own-group bias for women, and that small sample sizes likely was the reason why other studies (e.g., Lewin & Herlitz, 2002; McKelvie et al., 1993) only found an advantage favoring women on female faces. Here, the mini-meta-analysis of effect sizes across Studies I-IV, based on a total number of 492 participants, showed that there was no sex difference in memory for

male faces (see Table 2). Thus, it is unlikely that the presence of a female advantage on male faces is a question of power; there is likely another explanation. Indeed, in the CFMT, six male faces presented in different views are learned. Recognition of these faces is tested in three different tasks, each requiring the selection of the target among two distractors. In these tasks, the same encoded images of targets, novel images of targets (e.g., altered view), and novel images of the targets with visual noise added are presented together with lure faces. Unfortunately, Bowles et al. (2009) did not report men and women's performance on the various recognition conditions separately, but it may be the case that women's advantage over men was not present on the easiest recognition task, but only on the more difficult tasks (cf. Godard & Fiori, 2012; McBain et al., 2009). Thus, women seem to outperform men on male faces when the task depends on sensitivity to low spatial frequency (configural) information. Moreover, in the CFPT, the task is to sort a number of morphed faces depending on their similarity to a target face, which is also similar to the identity discrimination task used by McBain et al. (2009). Thus, under certain conditions, women have an advantage over men in perceptual processing and memory for male faces, but mainly when visual noise has been added to the images, when the picture of the target has been altered between encoding and test, and when fine-grained discrimination of an individual's identity is required.

Conclusion: In face of these findings, it is difficult to conclude that women's advantage over men only is found in perceptual processing and memory for female faces. In turn, women's own-gender bias in memory for faces may not completely account for the findings of a sex difference in memory for female faces. Women seem to have a more general advantage compared to men in processing and memory for faces, which is also in line with fMRI findings (e.g., Golarai et al., 2010).

4.7.2 The potential role of expertise

The results of Study II and IV suggest that mechanisms of women's own-gender bias and the sex difference may be somewhat different, both with respect to the effects of divided attention, and to the patterns of men and women's BOLD responses to faces. On the other hand, the exact same patterns may not be expected, given that one effect is found within individuals (women's own-gender bias) and the other between (sex difference in memory for female faces).

The results reviewed in the Introduction and in section 4.6.1 suggest that women also have an advantage over men on facial discrimination and recognition tasks that is not limited to female faces (Bowles et al., 2009; McBain et al., 2009; Megreya et al., 2011). In addition, the findings of sex differences in BOLD and event-related potential responses to faces suggest that men and women may process faces somewhat differently (Golarai et al., 2010; Proverbio et al., 2006; Proverbio et al., 2010; Tahmasebi et al., 2012). Taken together, this suggests that women have a greater expertise for faces than men, which is particularly marked for female faces, as women may be more proficient at processing female compared to male faces. In turn, women would be expected to show a higher degree of holistic and featural processing of faces compared to men, and particularly for female faces. This does not necessarily mean that socio-cognitive mechanisms (e.g., a higher motivation to encode one material

compared to another) are not involved when women encode female and male faces, as expertise most likely would imply a greater interest in the material one is an expert on, and more attention is paid to the details.

However, a perceptual expertise account may not be sufficient. Why would there be a sex difference in face processing and recognition that is not merely a result of women showing an own-gender bias? As mentioned in the Introduction, there are early sex differences in orientation to faces versus other objects, in the extent to which girls and boys engage in eye-to-eye contact with the mother and other individuals, particularly females, and females seem to be more protected from disorders related to impaired face processing and recognition such as autism spectrum conditions (for a review, see Baron-Cohen et al., 2011). These findings suggest that there may be genetic and/or prenatal hormonal factors that influence the degree of orientation to faces and the development of face processing, which may make females somewhat more likely than males to show a higher degree of orientation to faces. In turn, this may result in females developing a neural system more tuned to face processing. Moreover, females' face processing skills would be especially tuned to female faces, as infants learn to discriminate between female faces before male faces (Ramsey et al., 2005; Ramsey-Rennels & Langlois, 2006), and girls may continue to be more oriented towards other females, while boys may be more likely to orient themselves to other males during childhood. However, it is not clear whether boys are more likely to show an own-gender bias during adolescence, and why men (at the group level) do not seem to show a gender bias at all during adulthood. It may be the case that during late adolescence and in adulthood, there is a large variation in men's experience with female and male faces, or, men (as a group) may be equally likely to individuate between females and males. Of interest would be to assess whether male individuals showing an own- or other-gender bias on one test consistently also show a bias in this direction across several other recognition memory tests, which could point to whether this is a stable performance pattern on the individual level. In turn, potential reasons for the presence or no presence of a male gender bias in memory for faces could be better addressed.

For women, it may not simply be the case that their assumed early expertise "remains" in adulthood, but that their presumed expertise for female faces, and maybe faces in general, is continuously updated and maintained as they continue to actively individuate between females. There are findings suggesting that memory biases for a category of faces is highly dependent on short-term previous experience (e.g., Hills, 2012; for a review, see Macchi Cassia, 2011), and in line with this, short-term individuation practice with other-race faces can reduce the own-race bias in memory (McGugin et al., 2011; Tanaka & Pierce, 2009). Thus, it is likely that current facial experience is guided by previous experiences, and will probably guide future experiences.

4.8 METHODOLOGICAL CONSIDERATIONS AND LIMITATIONS

4.8.1 Variations in sex hormone levels

Within-individual levels of sex hormones vary substantially: with age (pre- and postnatally, adrenarche, gonadarche, menopause; and as shown in Study I, between ages 12-14), situational factors (stress, exercise), time of year, and shows a cyclic

pattern (in women, approximately a monthly cycle; in men, a daily and a seasonal cycle; Dabbs, 1990; Sherman & Korenman, 1975; Silverman et al., 1999; Valero-Politi & Fuentes-Arderiu, 1998). In Study I, some participants were tested in the spring and others during the fall; however, complementary analyses (data not shown) indicated that the levels of hormones were not different depending on season. Another related issue is that girls who had reached menarche were tested at different days of their menstrual cycle. The additional analyses did not reveal any systematic influence on cognitive performance, although E_2 levels were lower during the follicular compared to the luteal phase, as expected.

4.8.2 Difference scores

In Study IV, difference scores were used. The use of difference scores has been criticized, as this type of measure has issues with reliability (Cronbach & Furby, 1970). To illustrate this, think of for instance the test-retest reliability for face recognition memory, which in some studies has been found to be of moderate size (e.g., 0.63, O'Bryant, Hilsabeck, McCaffrey, & Gouvier, 2003). This means that a significant amount of error may be introduced when difference scores are formed based on such measures. It may be worrying that difference scores for own-group biases seem to be somewhat unreliable (e.g., Slone et al., 2000), but nevertheless, a reliable relation between differences in BOLD responses of left FFG and memory for female and male faces was found in Study IV.

4.8.3 Localizer task and statistical thresholds

One concern is that no localizer task was included in Study IV. Complex contrast stimuli, such as chairs, antique radios, or other objects are typically used to define face-specific BOLD responses in FFG and IOG (for an overview, see Berman et al., 2010). In Study IV, the contrast stimulus was three X's, which arguably is less complex than for instance chairs. Even though a previous study indicated that a simple baseline task as well as a localizer task resulted in very similar definitions of individuals' FFAs (Lehmann et al., 2004), some individuals' peak activations in Study IV were located in posterior FFG, in contrast to the more typical observation that FFAs are located in mid-FFG (Berman et al., 2010). Therefore, additional control analyses were run on data extracted from ROIs that only included BA37 in FFG, which showed that the results were equivalent.

The use of uncorrected statistical thresholds when assessing BOLD responses may be an issue, as appropriate thresholds should be set to avoid Type I errors. In Study IV, we used a ROI-based approach, with an uncorrected threshold ($p < .0001$) and a cut-off of at least 8 contiguous activated voxels, in accordance with previous studies (e.g., Minnebusch, Suchan, Köster, & Daum, 2009). For four subjects, the statistical threshold had to be relaxed in order to find significantly activated clusters in IOG. This seems to be a general problem with individually defined ROIs, as the threshold can be too strict for defining ROIs in certain individuals, but at the moment, there are no perfect guidelines for how face-specific ROIs should be defined on an individual basis (Rossion, Hanseeuw, & Dricot, 2012). On the other hand, the use of individual ROI definitions seems preferable as compared to defining ROIs based on group activation

maps, especially in larger areas such as FFG and IOG, showing large individual differences in location of peak voxel activation and cluster size.

4.8.4 Materials and participants

In Study III, Swedish and Bangladeshi faces were used, but only Swedish participants were included. Rehnman and Herlitz (2007) also assessed memory for Swedish and Bangladeshi faces in a Swedish sample, and obtained a similar performance pattern with a magnified own-race bias for female faces. Whether the set of Bangladeshi faces and Swedish participants may be special as compared to participants and faces of other ethnicities should be clarified in future studies. In any case, a female own-gender bias in face recognition was found in Study III, which also has been found in studies conducted in China (Ino et al., 2010), Great Britain (Wright & Sladden, 2003), and the US (O'Toole et al., 1998; Slone et al., 2000), suggesting that at least this effect seems to be general across various cultural contexts.

4.9 FUTURE DIRECTIONS

The findings of the present study indicated that girls' advantage over boys in memory for female faces was not increased between ages 12-14, and the sex difference was not larger in individuals with higher levels of sex hormones or more advanced pubertal maturation (relative to their age group). Additional analyses also indicated that girls' advantage over boys in memory for female faces was not a result of girls' higher verbal episodic memory. Findings of Study II indicated that women's own-gender bias is not a result of more elaborate processing of female compared to male faces during encoding, which would have required working memory processing. Further, controlling for facial attractiveness did not reduce women's own-gender bias (Study III), and women showed a higher BOLD response to female than male faces in FFG and IOG (Study IV).

These findings suggest that women process female faces more efficiently than male faces during encoding, which may be a result of perceptual expertise for female faces. One suggested marker of perceptual expertise is that experts preferentially categorize their objects of expertise at a more specific level than novices (Tanaka & Taylor, 1991). Interestingly, studies investigating classification of own- and other-race faces at the more basic level of face ethnicity have shown that own-race faces are classified slower and sometimes even less accurately than other-race faces (e.g., Feng et al., 2011). Of interest is that women seem to categorize male faces by gender faster than female faces (O'Toole et al., 1998; van Wingen, Mattern, Verkes, Buitelaar, & Fernandez, 2008; but see Hoss, Ramsey, Griffin & Langlois, 2005). An additional marker of expertise is the reliance on configural information while processing objects-of-expertise (Diamond & Carey, 1986), although expertise may also be related to better processing of features (e.g., Hayward et al., 2008). It would be of interest to assess whether such potential markers of face expertise are also observed for women's processing of female versus male faces, and in relation to men. In addition, why is women's advantage over men in identification and memory for male faces only found on certain tasks? This suggests that women may be more sensitive than men to low spatial frequency information in faces (i.e., the rough facial configuration), and it would be of interest to assess potential sex differences in the subcortical route for face processing. This could give us a better idea of whether efficiency of this system is related to women's advantage on these

tasks. I also believe that it would be informative to systematically assess potential sex differences in effective connectivity between regions of the core face network during face processing, with a particular focus on face gender (see also Mather et al., 2010). We also need to address the possibility that women's ability to encode (female) faces may be more sensitive than men's to manipulations, such as divided attention, and why this may be the case.

I am of the firm belief that it would be fruitful to use a developmental framework to understand females' own-gender bias and sex differences in perception and memory for faces, and instead of testing many different individuals, increase the number of measurement occasions for the same individuals. Important longitudinal measures would be structural data of the brain, fMRI and/or EEG data, hormonal assays, measures of pubertal development, and naturally, a wide variety of behavioral measures related to face processing and recognition, but also to other important measures of cognitive development (e.g., executive functions, attentional processing, episodic memory for other materials than faces). Using such an approach, it may be possible to tease apart and assess interactions between biological maturation (in terms of pubertal maturation), development of brain structures, general cognitive development (e.g., improvement of executive functions), and the development of an increasingly more specific neural system for face processing.

As noted by Field and colleagues (1984), commenting on their findings of that neonatal girls showed a larger novelty preference than boys for an unfamiliar female face compared to their mother's face: "The sex difference in this study merely contributes to what Cohen and Gelber (1975) have labeled a most confusing and contradictory literature" (p. 24). Focusing on individual development, a longitudinal approach combined with experimental data collections would hopefully resolve many of the problems and inconsistencies found in cross-sectional studies addressing the development of face processing and recognition, as well as the development of the female own-gender bias and sex differences in perception and memory for faces.

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7 APPENDIX

List of dissertations from the Aging Research Center and the Stockholm Gerontology Research Center, 1991-2012.

1991

Herlitz Agneta. Remembering in Alzheimer's disease. Utilization of cognitive support.

1992

Borell Lena. The activity life of persons with a dementia disease.

1993

Fratiglioni Laura. Epidemiology of Alzheimer's disease. Issues of etiology and validity.

Almkvist Ove. Alzheimer's disease and related dementia disorders: Neuropsychological identification, differentiation, and progression.

Basun Hans. Biological markers in Alzheimer's disease. Diagnostic implications.

1994

Grafström Margareta. The experience of burden in care of elderly persons with dementia. (Karolinska Institutet and Umeå University)

Holmén Karin. Loneliness among elderly - Implications for those with cognitive impairment. (Umeå University)

Josephsson Staffan. Everyday activities as meeting-places in dementia.

Stigsdotter-Neely Anna. Memory training in late adulthood: Issues of maintenance, transfer and individual differences.

Forsell Yvonne. Depression and dementia in the elderly.

1995

Mattiasson Anne-Cathrine. Autonomy in nursing home settings.

Grut Michaela. Clinical aspects of cognitive functioning in aging and dementia: Data from a population-based study of very old adults.

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Wahlin Åke. Episodic memory functioning in very old age: Individual differences and utilization of cognitive support.

Wills Philippa. Drug use in the elderly: Who? What? & Why? (Licentiate thesis)

Lipinska Terzis Beata. Memory and knowledge in mild Alzheimer's disease.

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Almberg Britt. Family caregivers experiences of strain in caring for a demented elderly person (Licentiate thesis)

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Agüero-Eklund Hedda. Natural history of Alzheimer's disease and other dementias.

Guo Zhenchao. Blood pressure and dementia in the very old. An epidemiologic study.

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Cornelius Christel. Drug use in the elderly - Risk or protection? Findings from the Kungsholmen project

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Palmer Katie. Early detection of Alzheimer's disease and dementia in the general population. Results from the Kungsholmen Project.

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Ngandu Tiia. Lifestyle-related risk factors in dementia and mild cognitive impairment: A population-based study.

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Marengoni Alessandra. Prevalence and impact of chronic diseases and multimorbidity in the aging population: A clinical and epidemiological approach.

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Fors Stephan. Blood on the tracks. Life-course perspectives on health inequalities in later life.

Keller Lina. Genetics in dementia. Impact of sequence variations for families and populations.

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Caracciolo Barbara. Cognitive impairment in the nondemented elderly: Occurrence, risk factors, progression.

Rieckmann Anna. Human aging, dopamine, and cognition. Molecular and functional imaging of executive functions and implicit learning.

Schön Per. Gender matters. Differences and change in disability and health among our oldest women and men.

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Haasum Ylva. Drug use in institutionalized and home-dwelling elderly persons.

Mangialasche Francesca. Exploring the role of vitamin E in Alzheimer's disease: An epidemiological and clinical perspective.